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# SEED MORPHOLOGY AND ANATOMY OF RHIZOPHORACEAE, INTER- AND INFRAFAMILIAL RELATIONSHIPS<sup>1</sup>

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## ABSTRACT

*We present an overall study of the seed morphology and anatomy of all Rhizophoraceae (10 inland and 4 mangrove genera). Morphologically seeds are arillate, winged or nonappendaged; both arillate and winged seeds are borne in capsular fruits, and nonappendaged seeds in baccate or indehiscent hard-walled capsules. Seed coat anatomy is diversified in correlation with the seed and fruit morphology, but a well-developed exotesta and a fibrous exotegmen are common to all inland genera. Despite certain minor divergences, the seed coat of different genera of Rhizophoraceae is defined as exotestal, exotestal-exotegmic, or undifferentiated. Different combinations of seed morphological and anatomical features characterize different genera or groups of genera. An overall comparison of seeds and other reproductive characters confirms that in Rhizophoraceae arillate seeds and the presence of a fibrous exotegmen are plesiomorphic features that can be used in searching for related families. Seed morphology and anatomy also support grouping Rhizophoraceae with Elaeocarpaceae and Celastraceae, and the exclusion of Elaeocarpaceae from Malvales. Our comparison further suggests that the seed morphology and anatomy of Rhizophoraceae have evolved as the result of adaptation to different methods of seed dispersal from ant dispersal to dispersal by wind, bird, mammal, or water. We carried out a cladistic analysis of the genera of Rhizophoraceae on the basis of 16 reproductive characters (including those of seed morphology and anatomy). Blepharistemma, Cassipourea, Comiphyton, Anopyxis, Macarisia, and Sterigmapetalum, all inland genera that have been assigned to Macarisieae, are characterized by having many plesiomorphies (particularly a superior ovary). The last three genera have winged seeds and a thinner seed coat (apomorphies), whereas the first three have arillate seeds. Among the four remaining inland genera, which have been assigned to Gynotrocheae, Crossostylis (with arillate seeds) differs greatly from the others in having only one apomorphy (i.e., an inferior ovary); it retains many plesiomorphies. In contrast, Carallia, Gynotroches, and Pellacalyx share a nonappendaged seed and a persistent meso- and endotegmen, both clearly synapomorphies, and Gynotroches and Pellacalyx further share some distinct synapomorphies, suggesting their close affinities. The four mangrove genera—Bruguiera, Ceriops, Kandelia, and Rhizophora—which have been segregated as Rhizophoreae, share many synapomorphies (e.g., an undifferentiated seed coat and the complete lack of the tegmen), and therefore the coherence of Rhizophoreae is not in doubt. Cladistically the mangrove genera are more closely related to Carallia, Gynotroches, and Pellacalyx than to Macarisieae. Based on our cladistic analysis, the traditional infrafamilial classification is revised, and a new tribe Crossostylideae, which consists of Crossostylis only, is proposed.*

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Traditionally, Rhizophoraceae have been broadly defined to contain one mangrove tribe Rhizophoreae (4 genera) and three inland tribes: Macarisieae (6 genera), Gynotrocheae (4 genera), and Anisophylleae (4 genera) (e.g., Melchior, 1964). The comparative study of wood anatomy (van Vliet, 1976) and leaf architecture and anatomy (Keating & Randrianasolo, this volume; Baas, pers. comm.)

has supported this broad definition of the family. In contrast, embryological evidence (Tobe & Raven, 1983), as well as an overall comparison based on various systematic characters (Dahlgren & Thorne, 1984), strongly suggested that the overall group was heterogeneous and indicated the need for further embryological studies of the constituent genera and tribes as an important key to their

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<sup>1</sup> The study was supported by grants from the U.S. National Science Foundation to P. H. Raven, most recently BSR-8518902. We are grateful to Ann Bird, Barbara Browning, Lorence Dorr, Jack Fisher, K. Gopinathan Nair, Peter C. Hoch, Betsy R. Jackes, L. Liben, K. S. Manilal, Gordon McPherson, Bruce W. Nelson, Juan V. Pancho, Ching-I Peng, N. Sasidharan, Benjamin C. Stone, Duncan W. Thomas, and Robert Wingfield for collecting the materials that were used in this study.

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relationship. Earlier embryological studies were limited to 9 of 18 genera: *Bruguiera*, *Ceriops*, and *Rhizophora* of Rhizophoreae (Karsten, 1891; Cook, 1907; Carey, 1934; Mauritzon, 1939; Juncosa, 1982, 1984b); *Cassipourea* of Macarisieae (Juncosa, 1984a); *Carallia* and *Gynotroches* of Gynotrocheae (Karsten, 1891; Haberlandt, 1895; Mauritzon, 1939; Corner, 1976); and *Anisophyllea*, *Combretocarpus*, and *Poga* of Anisophylleae (Karsten, 1891; Hou, 1958; Vaughan, 1970; Geh & Keng, 1974). Most of these studies were concerned with relatively few embryological features.

Thus we recently presented an overall embryological study of "Anisophylleae" (Tobe & Raven, 1987b) and, with support of evidence from other sources, justified the separation of Anisophylleaceae as a distinct family from the rest of Rhizophoraceae, as proposed earlier by several authors (e.g., Ridley, 1922; Cronquist, 1981, 1983; Dahlgren, 1983). Subsequently, we presented the first comprehensive embryological study on two inland genera, *Cassipourea* and *Sterigmapetalum* of Macarisieae (Tobe & Raven, 1987a), which were recently separated from Macarisieae as constituting a new tribe Hypogyneae (Steyermark & Leisner, 1983), and we provided some discussion on infrafamilial relationships based on data available. Juncosa (pers. comm.) has surveyed the respective embryological features of the remaining tribes, Gynotrocheae and Rhizophoreae. Consequently, Rhizophoraceae are becoming one of the most well-known families with respect to their embryological characters.

Previous embryological studies of Rhizophoraceae have lacked comprehensive, comparative information on the seed morphology and anatomy of the whole family. Concerning the seed morphology, Schimper (1893), Hou (1958, 1968), Floret (1974, 1976), and Tobe & Raven (1987a) described some of the constituent genera and suggested that Rhizophoraceae are diverse in this feature. However, no overall studies, except for the preliminary discussions in our previous paper (Tobe & Raven, 1987a), have been made.

Carey (1934) provided fragmentary descriptions on the seed coat anatomy of *Rhizophora* and *Ceriops* of Rhizophoreae. Later, Corner (1976) described some details of the seed coat anatomy of *Carallia*, *Gynotroches*, and *Pellacalyx* (all Gynotrocheae); Tobe & Raven (1987a) described those of *Cassipourea* and *Sterigmapetalum* of Macarisieae; and Juncosa studied those of *Carallia* and *Gynotroches*. These works contained impor-

tant suggestions inducing further studies. For example, Corner (1976, 1: 161) defined the seed coat of both *Gynotroches* and *Pellacalyx* as "exotegmic," with the exotegmen fibrous and, on the basis of seed coat anatomy, transferred the two genera into Legnotidaceae, a family first described by Endlicher (1840) as "Legnotidae" to comprise *Cassipourea* and *Gynotroches*. Tobe & Raven (1987a) showed that *Cassipourea* and *Sterigmapetalum* (Macarisieae) have a thick and a thin testa, respectively, and are clearly distinct from each other based on seed coat anatomy. Juncosa (pers. comm.) reports that the seed coat of *Carallia borneensis* differs from those of other inland genera in having no persistent tegmen and a vascularized testa. Thus, the works of Corner (1976), Tobe & Raven (1987a), and Juncosa strongly suggested the utility of seed coat anatomy in considering relationships of genera in Rhizophoraceae and indicated that an overall study of seed coat anatomy was needed for further understanding of infrafamilial relationships. The utility of the seed morphology and anatomy in such considerations has already been demonstrated in studies on several unrelated families (e.g., Cruciferae—Vaughan & Whitehouse, 1971; Polygalaceae—Verkerke, 1985), leading to a revision of conventional tribal classifications in each case.

This paper presents the features of seed morphology and anatomy for the whole family Rhizophoraceae, which consists of 14 genera (excluding the genera of Anisophylleaceae). These results, which have revealed a considerable degree of diversity in these features, are then used together with other evidence to clarify infrafamilial phylogenetic relationships. Dahlgren (this volume) has used these features extensively in searching for relatives, and this analysis is of fundamental importance for such comparisons.

#### MATERIALS AND METHODS

Twenty-one species representing all 14 genera of Rhizophoraceae were investigated. Collection data are provided in Table 1. For microscopic observations mature and immature seeds were microtome sectioned following standard paraffin methods described elsewhere (Tobe & Raven, 1987b). Some hard specimens, like those of *Ceriops*, were embedded in glycol methacrylate, sectioned with glass knives, and stained with 0.1% Toluidine Blue (e.g., Figs. 28, 29). Scanning electron micrographs were also used in observing seeds of *Gynotroches* and *Pellacalyx*, and they were prepared following the standard method using a JEOL 25S instrument



TABLE 1. Studied taxa, collections, and materials. Asterisk (\*) indicates that dry herbarium materials were investigated. Tribal positions of genera follow Melchior (1964) and Floret (1976).

Taxa	Collections and Materials
Macarisieae	
<i>Anopyxis klaineana</i> (Pierre) Engl.	Cameroon. <i>D. Thomas</i> 3464 (MO)—buds & fruits
<i>Blepharistemma membranifolia</i> (Miq.) Ding Hou	India. Quilon, Kerala, <i>K. Manilal</i> s.n. in 1984 (MO)—female buds India. Grichur District, Kerala, <i>N. Sasidharan</i> s.n. in 1986 (MO)—fruits
<i>Cassipourea gummiflua</i> Tul. var. <i>verticillata</i> (N. E. Br.) J. Lewis	Zimbabwe. Cultivated, National Botanic Garden, Harare, <i>Th. Müller</i> 3558 (SRGH); original collection: Mt. Inyangani, <i>Th. Müller</i> 698 (SRGH)—buds and fruits
<i>C. guianensis</i> Aubl.	Brazil. Manaus, <i>B. Nelson</i> 1324 (MO, NY)—buds & fruits
<i>C. malosana</i> (Bak.) Alston	Zimbabwe. Cultivated, National Botanic Garden, Harare, <i>Th. Müller</i> 3557 (SRGH); original collection: Chirinda Forest, Mt. Selinda, <i>B. Goldsmith</i> —buds & fruits
* <i>Comiphyton gabonense</i> (J.-J. Floret)	Zaire. Mt. Homas, Irumu, <i>Germain</i> 5213 (BR)—fruits
<i>Macarisia pyramidata</i> Thou.	Madagascar. <i>L. Dorr</i> 4392 (MO)—fruits
<i>Sterigmapetalum heterodoxum</i> Steyermark & Liesner	Venezuela. Sierra de San Luis, Falcón, <i>R. Wingfield</i> 13692 (MO)—female buds, 13696 (MO)—fruits
Gynotrocheae	
<i>Carallia brachiata</i> (Lour.) Merr.	Australia. Jourama Falls National Park, North Queensland, <i>B. Jackes</i> s.n. in 1983 (JCT)—buds & fruits
<i>C. eugenioidea</i> King.	Malasia. Selangor, <i>B. Stone</i> 15114 (KLU)—buds & fruits
* <i>Crossostylis biflora</i> Forst.	Society Islands. Tahaa, Mt. Purauti, <i>H. St. John</i> 17346 (MO)—fruits
<i>C. grandiflora</i> Brongn. & Gris	New Caledonia. <i>G. McPherson</i> 6331 (MO)—buds & fruits
* <i>C. multiflora</i> Brongn. & Gris	New Caledonia. Thy River valley, ca. 12 km NE Noumea, <i>G. McPherson</i> 1617 (MO)—fruits
<i>Gynotroches axillaris</i> Bl.	Malaysia. Maxwell Hill, Perak, <i>B. Stone</i> 15397 (KLU)—buds & fruits
<i>Pellacalyx lobbii</i> (Hook. f.) Schimp.	Malaysia. Sarawak, <i>P. Chai</i> s.n. in 1986, no voucher—fruits
<i>P. cf. saccardianus</i> Scort.	Malaysia. Maxwell Hill, Perak, <i>B. Stone</i> 15396 (KLU)—buds & fruits
Rhizophoreae	
<i>Bruguiera gymnorrhiza</i> (L.) Lam.	Mozambique. Maputo, Costa do Sol, <i>J. de Koning</i> & <i>M. C. Groenaedyk</i> 9243 (LMU)—buds & fruits
<i>Ceriops tagal</i> (Perr.) C. B. Rob.	Malaysia. Port Klang, Selangor, <i>Mahmud Sider</i> s.n. in 1983, no voucher—buds & fruits Philippines. Dagbilao, Quezon, Luzon, <i>Hernaez CA</i> 29249 (CAHUP)—buds
<i>Kandelia candel</i> (L.) Druce	Republic of China (Taiwan). Tanshuei, Taipei Co., <i>C. Peng</i> 4504 (HAST)—buds & fruits
<i>Rhizophora mangle</i> L.	U.S.A. Cultivated, Fairchild Tropical Garden, Florida. <i>H. Tobe</i> s.n. in 1981, no voucher—buds & fruits
<i>R. stylosa</i> Griff.	U.S.A. Cultivated, Fairchild Tropical Garden, Florida. <i>FG</i> 69-111. <i>H. Tobe</i> s.n. in 1981, no voucher—buds; <i>A. Bird</i> s.n. in 1983, no voucher—fruits

(Tobe & Raven, 1987b). Comparisons among genera were made on the basis of mature seeds, and when materials were available, seed coat ontogeny was investigated to understand the mature structure more completely. The terminology on seeds and seed coat anatomy follows Corner (1976) and Schmid (1986); Schmid elaborated Corner's terminology.

OBSERVATIONS

The seeds of rhizophoraceous genera have either an aril or a wing, or they lack appendages. Arillate seeds occur in *Blepharistemma*, *Cassipourea*, and *Comiphyton* (all in Macarisieae), which have loculicidally (?) or septicidally dehiscent or indeshiscent capsular fruits (Floret, 1976), and in *Cros-*



*sostylis* (Gynotrocheae), which has capsular fruits of unknown dehiscence mode. Winged seeds occur in *Anopyxis*, *Macarisia*, and *Sterigmapetalum* (all in Macarisieae), which have septicidally dehiscent capsular fruits (Floret, 1976; contrary to Floret, Arènes (1954) described fruit dehiscence in *Macarisia* as loculicidal, but we confirmed septicidal dehiscence in *M. pyramidata*). Nonappendaged seeds occur in *Carallia*, *Gynotroches*, and *Pellacalyx* (all in Gynotrocheae), which have baccate fruits, and in *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora* (all in Rhizophoreae), which have indehiscent hard-walled fruits. Both the aril and the wing develop as an outgrowth of the exostome: compare the young arillate seed of *Cassipourea malosana* (Figs. 1, 2) with the young winged seed of *Anopyxis klaineana* (Figs. 3, 4). In the case of the aril, a raphal tissue, which continues from the outer integument, may also join the aril formation; however, a funicular or hilar tissue never joins there. Therefore, as discussed in a previous paper (Tobe & Raven, 1987a), the aril and the wing are homologous to each other, and the histogenetic origin of both structures are regarded substantially as exostomal.

We have also confirmed that the seed coat anatomy correlates with the external seed morphology type (i.e., arillate, winged, and nonappendaged) and, in addition, that within the nonappendaged seed category the seeds of *Gynotroches* and *Pellacalyx* are distinct from those of *Carallia*, as already described by Corner (1976) to some degree. The details are documented below.

#### ARILLATE SEEDS

*Blepharistemma*. It has been previously uncertain whether *Blepharistemma* has an aril, a wing, or neither, because fruits and seeds of this genus are undescribed. We found for the first time that *B. membranifolia*, the only species of the genus, has a fleshy aril (Fig. 5), which covers nearly the upper half of the seed. The mature seed is ellipsoid, with a somewhat conspicuous raphe, and very slightly depressed toward the lateral side; it is 4.3–4.5 mm long and 2.4–2.5 mm thick, as measured from the raphe to antiraphe (R–A), and 2.2–2.3 mm thick from side to side (L–L) (see Tobe & Raven, 1987a, fig. 14, for directions of width measurement).

The oldest seed coat available is 0.20–0.22 mm thick in total, comprising the testa 135–142  $\mu$ m thick and the tegmen about 50  $\mu$ m thick. When the embryo sac is mature, the outer and inner integuments are 3–4 cells and 4–5 cells thick,

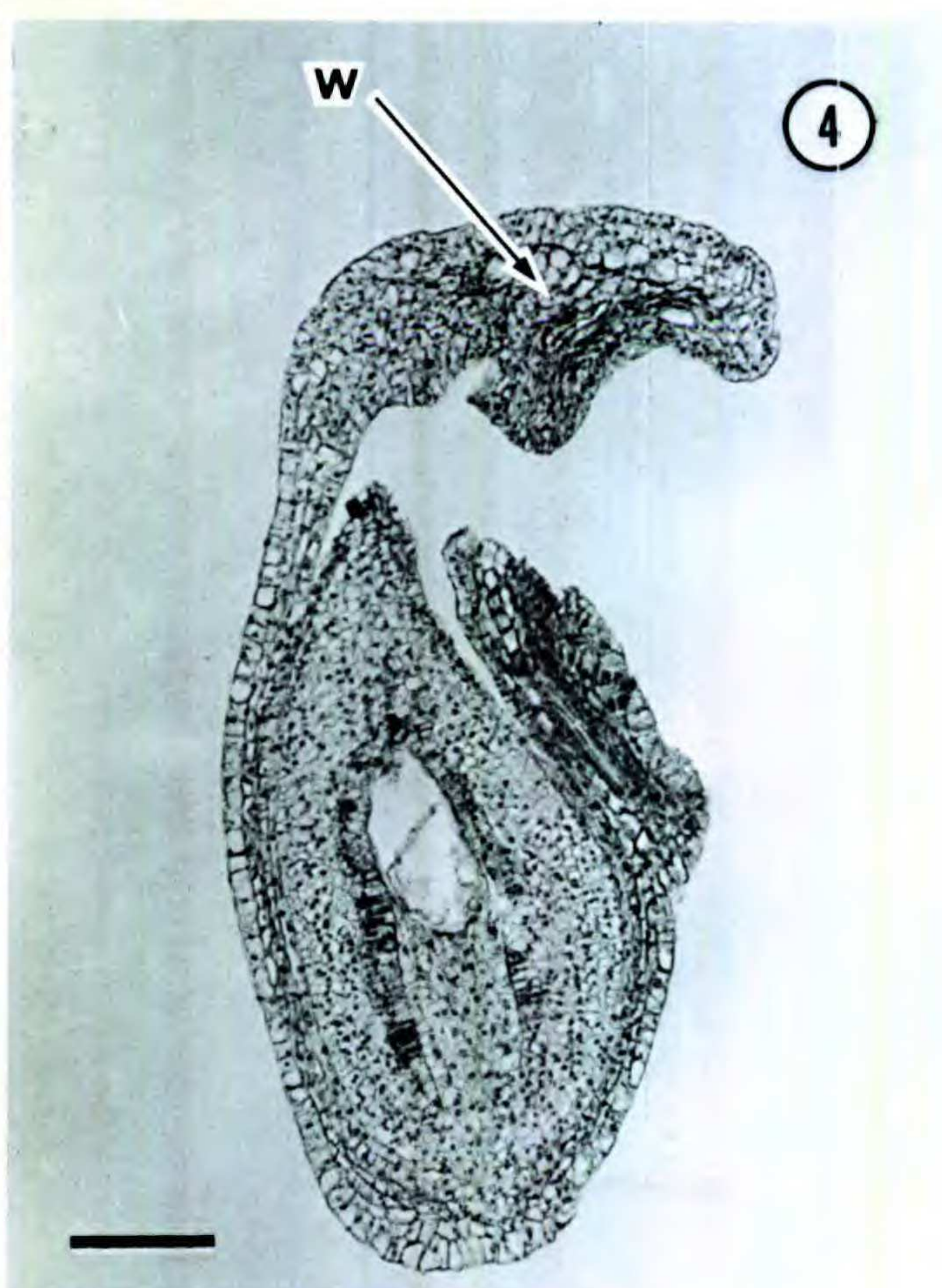
respectively. The outer integument increases its thickness in postfertilization stages and eventually differentiates into a 1-cell-layered exotesta, a 3–6-cell-layered mesotesta, and a 1-cell-layered endotesta (Fig. 6). There is no clear histological difference between the mesotesta and the endotesta. Exotestal cells are radially enlarged, thick-walled, and tanniferous, forming a palisade (Fig. 6). Meso- and endotestal cells are much smaller than the exotestal cells, but also somewhat thick-walled and tanniferous. The endotestal cells often contain crystals. On the other hand, the inner integument develops into a 1-cell-layered fibrous exotegmen and 2 or 3 underlying unspecialized cell layers, the latter of which apparently disintegrates further. (The seeds investigated in this study seem still somewhat immature, and we believe that the underlying cell layers below the exotegmen eventually disappear completely.) Of the constituent cell layers, the exotesta is the most conspicuously developed as a mechanical structure; therefore, the seed coat of *Blepharistemma* is exotestal.

*Cassipourea*. *Cassipourea* is a large and variable genus (4 subgenera and 80 species (Alston, 1925; Airy Shaw, 1973)), which shows a range of variation in seed size and anatomical structure. We described some details of seed size and seed anatomy earlier (Tobe & Raven, 1987a), and therefore these are only briefly summarized here. Only data on the total thickness of the mature seed coat were added.

The mature seed is ellipsoid (*Cassipourea guianensis* and *C. gummiiflua* var. *verticillata*) to broad ellipsoid (*C. malosana*) and slightly depressed to the raphe. In *C. guianensis*, the seed is 8.9–9.2 mm long and 2.6–2.8 mm thick (R–A) to 3.3–3.6 mm thick (L–L); in *C. gummiiflua* var. *verticillata* it is 4.2–4.4 mm long and 1.6–1.8 mm thick (R–A) to 2.2–2.4 mm thick (L–L); in *C. malosana* it is 5.0–5.2 mm long and 2.8–3.1 mm thick (R–A) to 4.5–4.8 mm thick (L–L). The aril is fleshy and wholly covers the seed except on the chalazal and antiraphe side.

In the three examined species, the mature seed coat is 0.16–0.22 mm thick in total and is composed of a 1-cell-layered exotesta, a 2–6-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen; all other cell layers of the tegmen are crushed and disappear, although both the outer and the inner integuments are multiple cell-layered at the mature embryo sac stage. The exotesta comprises enlarged cuboid, thick-walled cells; the meso- and endotesta are composed of much smaller cells, and endotestal cells may





FIGURES 1-4.—1, 2. Scanning electron micrograph (SEM) and longitudinal section (LS) of a mature ovule of *Cassipourea malosana* showing the early development of an aril.—3, 4. SEM and LS of a mature ovule of *Anopyxis klaineana* showing early development of a wing. All scales = 100  $\mu$ m. ar, aril; w, wing.



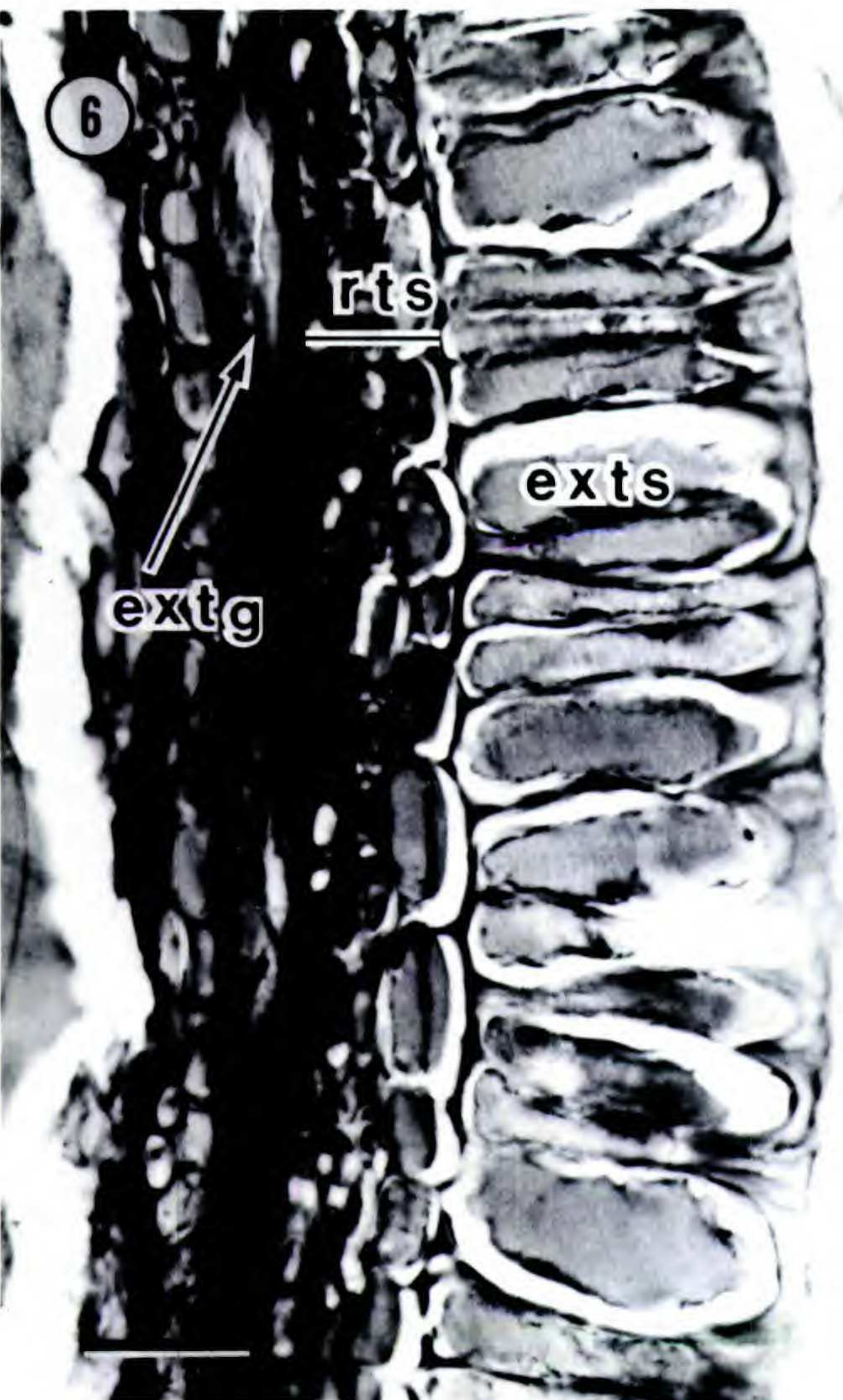
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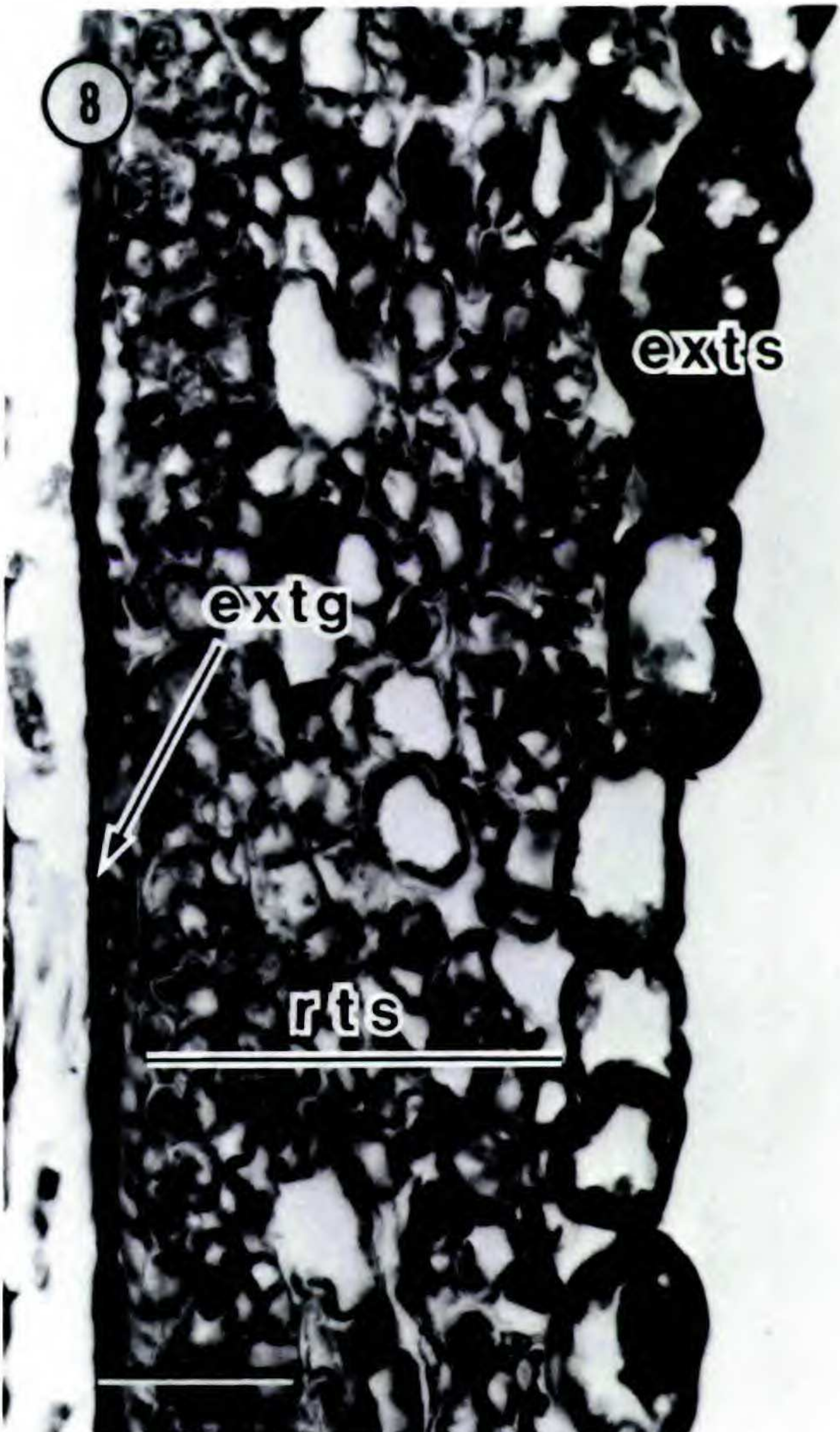
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contain crystals; the exotegmen is composed of longitudinally elongate, thick-walled fibrous cells. Testal cells are mostly tanniferous. In all three species, the exotesta is most conspicuously developed as a mechanical structure, and therefore the seed coat of *Cassipourea* is exotestal.

*Comiphyton*. The mature seed of the only species of the genus, *C. gabonense*, is narrowly ellipsoid (Fig. 7) and nearly circular in cross section; it is 7.0–7.5 mm long and 2.0–2.8 mm in diameter. The aril is restricted to a micropylar top, and its tissue is apparently irregularly folded (Fig. 7). Compared with those of the species examined of *Cassipourea*, the seed coat surface of *Comiphyton* is more undulated, although it is uncertain whether this difference distinguishes *Comiphyton* from all species of *Cassipourea*.

The mature seed coat is 0.14–0.18 mm thick in total and is composed of a 1-cell-layered exotesta, an 8–10-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen (Fig. 8). There is no clear difference between the mesotesta and the endotesta. The exotesta is composed of somewhat enlarged, thick-walled tanniferous cells; the meso- and endotesta comprise much smaller cells, and they do not contain crystals; the exotegmen is composed of longitudinally very narrow, fibrous cells. No other cell layers of the tegmen persist. Considering the structure of the entire seed coat, only the exotesta is relatively well developed as a mechanical structure. Therefore, the seed coat of *Comiphyton* is exotestal.

*Crossostylis*. The mature seeds of the three examined species, *C. biflora*, *C. grandiflora* (Fig. 9), and *C. multiflora*, are ellipsoid, bearing a raphe as a very narrow longitudinal ridge. The mature seed is 2.1–2.3 mm long and 1.4–1.6 mm in diameter in *C. biflora*; 3.6–3.8 mm long and 1.8–2.0 mm in diameter in *C. grandiflora*; and 1.8–1.9 mm long and 1.0–1.2 mm in diameter in *C. multiflora*. The aril is membranous, and its tissue is irregularly folded. The aril spreads over the micropylar top and does not tightly cover the seed proper.

The mature seed coat structure differs from species to species. In *Crossostylis grandiflora*, the mature seed coat is relatively thick—0.19–0.20 mm in total—and is composed of a 1-cell-layered

exotesta, a 2–3-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen (Fig. 10). There is no histological difference between the mesotesta and the endotesta. At the mature embryo sac stage, the outer and the inner integuments are 4–5 cells thick and 9–11 cells thick, respectively. As the seed matures, therefore, the inner integument completely disappears except for the outer epidermis—i.e., exotegmen—while the outer integument remains nearly persistent. The exotesta comprises enlarged, extremely thick-walled, tanniferous cuboidal cells; the meso- and endotesta are formed by unspecialized smaller cells; and the exotegmen is composed of longitudinally elongate, thick-walled, fibrous cells. Since the exotesta is most conspicuous as a mechanical structure, the seed coat of *C. grandiflora* is exotestal.

The mature seed coat structures of *Crossostylis biflora* (Fig. 13) and *C. multiflora* (Figs. 11, 12) are very similar. The total thickness is about 0.09 mm (*C. biflora*) or 0.06–0.07 mm (*C. multiflora*). The mature seed coat is basically composed of a 1-cell-layered exotesta, a 1-cell-layered mesotesta, a 1-cell-layered endotesta, and a 1-cell-layered exotegmen; however, the mesotesta and even the endotesta may be lacking in *C. multiflora* (Figs. 11, 12). Although we did not confirm the thickness of the integuments, they seem to be multiplicative, as we saw more clearly in our sample of *C. grandiflora*. The exotesta is covered with a thick cuticle; its cells are longitudinally elongate and contain tanninlike pigments. The meso- and endotestal cells are much smaller than those of the exotesta and contain crystals. The exotegmen is composed of extremely sclerotic, longitudinally elongate, fibrous cells. Compared with that of *C. grandiflora*, the exotegmen of these species is much more conspicuously developed as a mechanical structure. Therefore, the seed coat of *C. biflora* and *C. multiflora* is exotestal-exotegmic.

#### WINGED SEEDS

*Anopyxis*. The species examined, *A. klaineana*, has a large mature seed; it comprises the seed proper and a membranous wing (Fig. 14). The seed proper is oblanceoloid but extremely depressed laterally, and it is 13.4–13.7 mm long and 5.2–5.7 mm thick (R–A) to 1.6–2.1 mm thick (L–L). The

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FIGURES 5–8.—5, 6. Oldest arillate seed available of *Blepharistemma membranifolia* and longitudinal section (LS) of its seed coat.—7, 8. Mature arillate seed of *Comiphyton gabonense* and LS of its seed coat. Scales = 1 mm (Figs. 5, 7) and 50  $\mu$ m (Figs. 6, 8). exts, exotesta; rts, meso- and endotesta; extg, exotegmen.



wing is always larger than the seed proper and is 23.9–25.0 mm long and 10.6–11.4 mm wide.

The mature seed coat is thin and 0.09–0.11 mm thick; for the most part it is apparently composed largely of a 1-cell-layered exotesta and a 1-cell-layered exotegmen (Fig. 15). In the mature embryo sac stage, however, the outer and the inner integuments are 4–5 cells thick and 6–7 cells thick, respectively. As the seed matures, therefore, all integumentary cell layers except for the outer epidermis of both integuments seem to degenerate or collapse. The exotesta is composed of enlarged, thick-walled, tanniferous cells, and the exotegmen of longitudinally elongate, thick-walled, fibrous cells. Both the exotesta and exotegmen are conspicuous as mechanical layers, and therefore the seed coat of *Anopyxis* is exotestal-exotegmic.

*Macarisia*. The mature seed of this genus, like that of *Anopyxis*, comprises a seed proper and a membranous wing (Fig. 16). The size of seed varies within the genus; the species examined, *M. pyramidata*, is known to have the largest seeds in the genus (Arènes, 1954), which, however, are much smaller than those of *Anopyxis*. In *M. pyramidata*, the seed proper is ellipsoid but extremely depressed laterally as in other species of the genus; it is 3.5–3.9 mm long and 2.1–2.5 mm thick (R–A) to 0.4 mm thick (L–L). The wing is always larger than the seed proper and is 8.5–9.1 mm long and 3.6–4.2 mm wide.

The mature seed coat of *Macarisia pyramidata* is 0.05–0.07 mm thick in total, and it comprises mainly a 1-cell-layered exotesta and a 1-cell-layered exotegmen (Fig. 17). Crystalliferous (endotestal) cells may remain at places between the exotesta and the exotegmen (Fig. 17). We did not examine the thickness of integuments because we lacked material. The exotesta is composed of enlarged, thick-walled, and tanniferous cells; the

exotegmen comprises longitudinally elongate, thick-walled, fibrous cells. Based on *M. pyramidata*, the seed coat of *Macarisia* is exotestal-exotegmic.

*Sterigmapetalum*. Although the seed structure of this genus (consisting of seven species according to Steyermark & Liesner, 1983) has not been emphasized as a systematic character, it agrees with those of *Anopyxis* and *Macarisia* in having a seed proper and a membranous wing on the micropylar top. The morphology and anatomy of the mature seed of *S. heterodoxum* were discussed by Tobe & Raven (1987a). In this paper, only characteristic features of the species are briefly summarized, and data on the total thickness are added.

The seed proper is oblanceoloid and extremely depressed laterally; it is 5.0–6.0 mm long and 1.6–2.0 mm thick (R–A) to 0.8–1.0 mm thick (L–L). The wing is 7.4–10.2 mm long and 3.9–5.0 mm wide. (For other species of the genus, Steyermark & Liesner (1983) described the seeds of *S. obovatum* as oblong, plano-convex, 8 mm long and 3.5–4 mm wide.)

The mature seed coat is 0.08–0.10 mm thick in total and is composed only of a 1-cell-layered exotesta and a 1-cell-layered exotegmen, although the outer and the inner integuments were originally 2–4 cells thick and 8–10 cells thick, respectively. The exotesta comprises enlarged, somewhat radially elongate, thick-walled, tanniferous cells; the exotegmen is composed of longitudinally elongate, thick-walled, fibrous cells. The seed coat of *Sterigmapetalum* is exotestal-exotegmic.

#### NONAPPENDAGED SEEDS

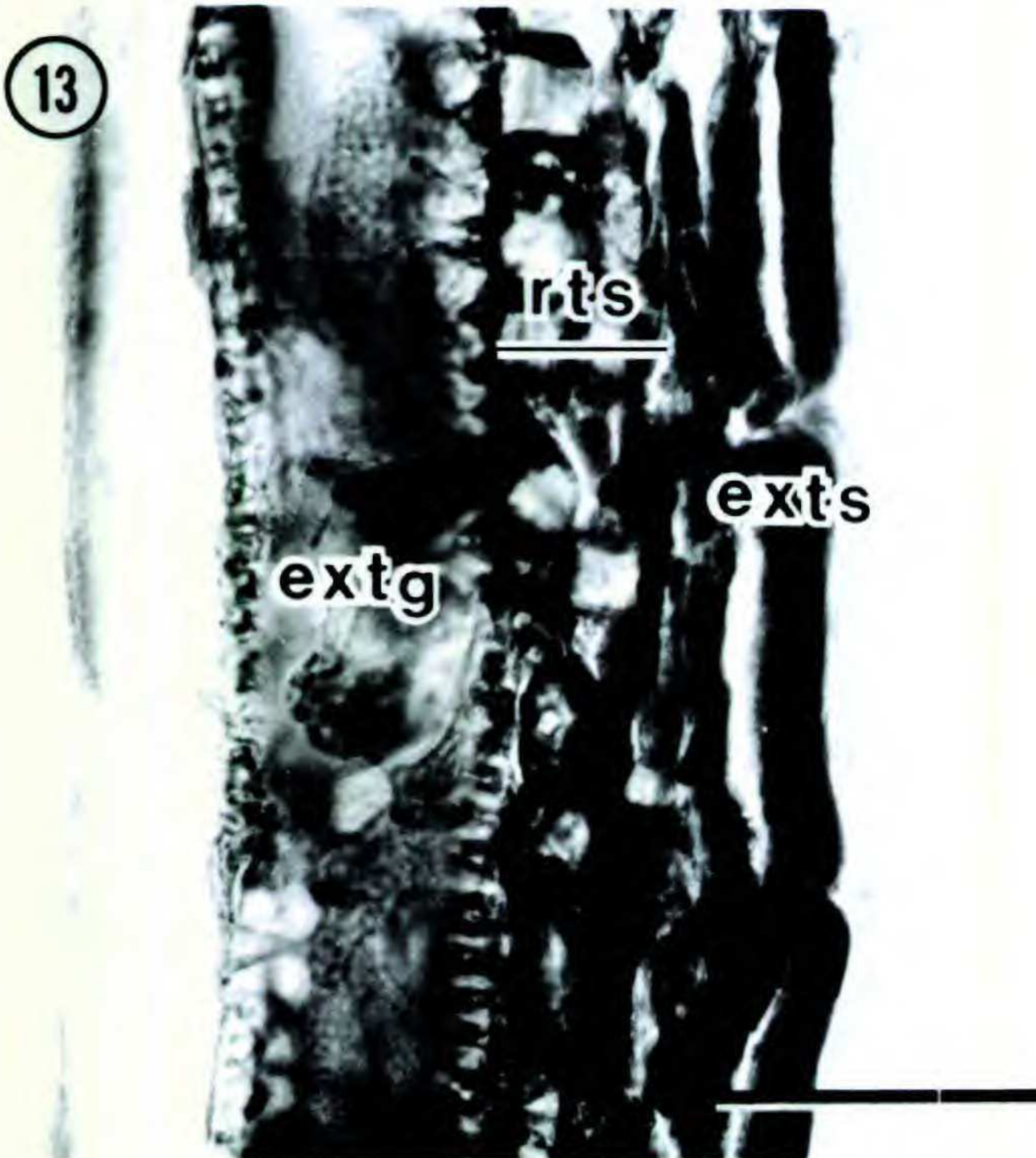
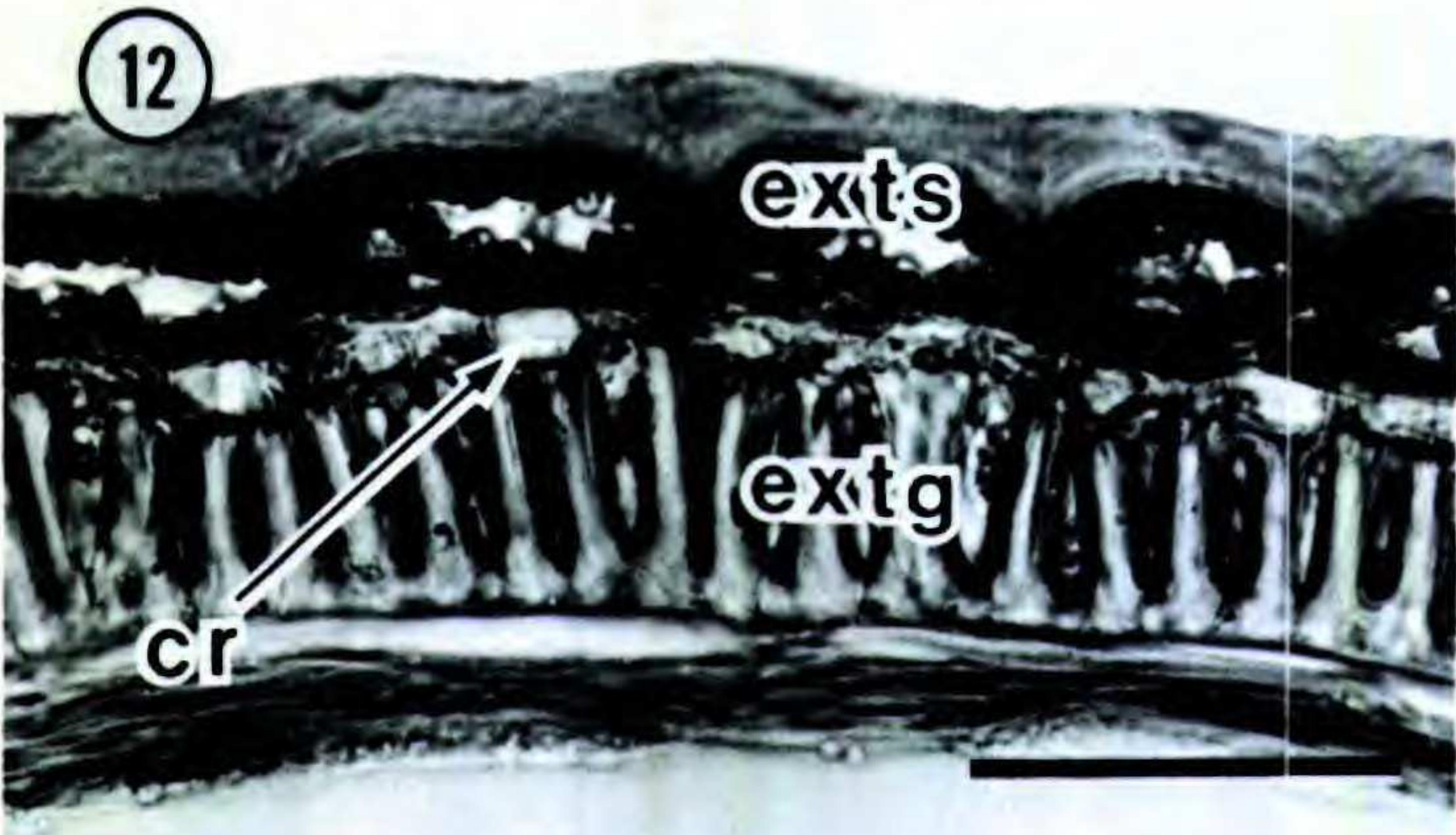
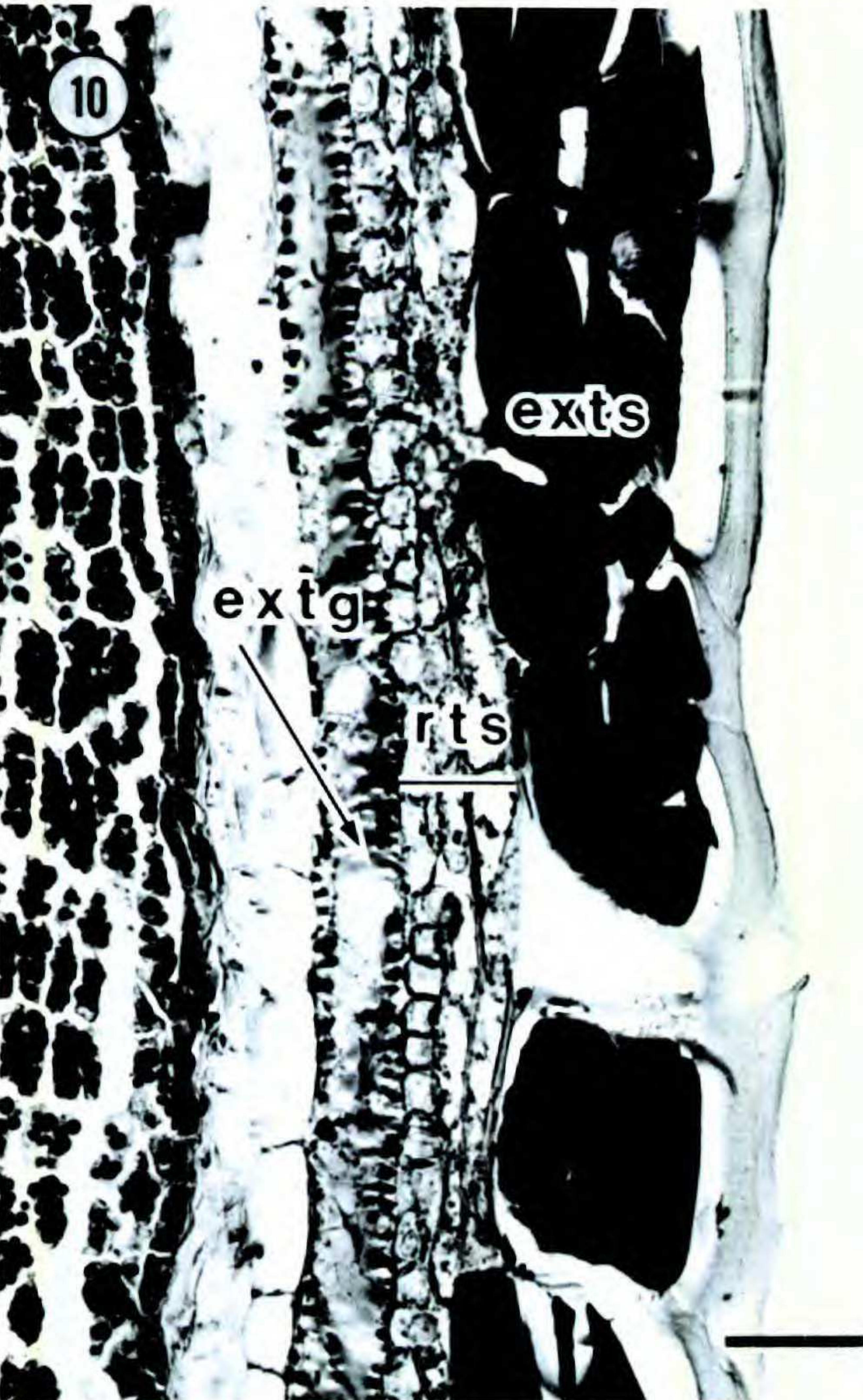
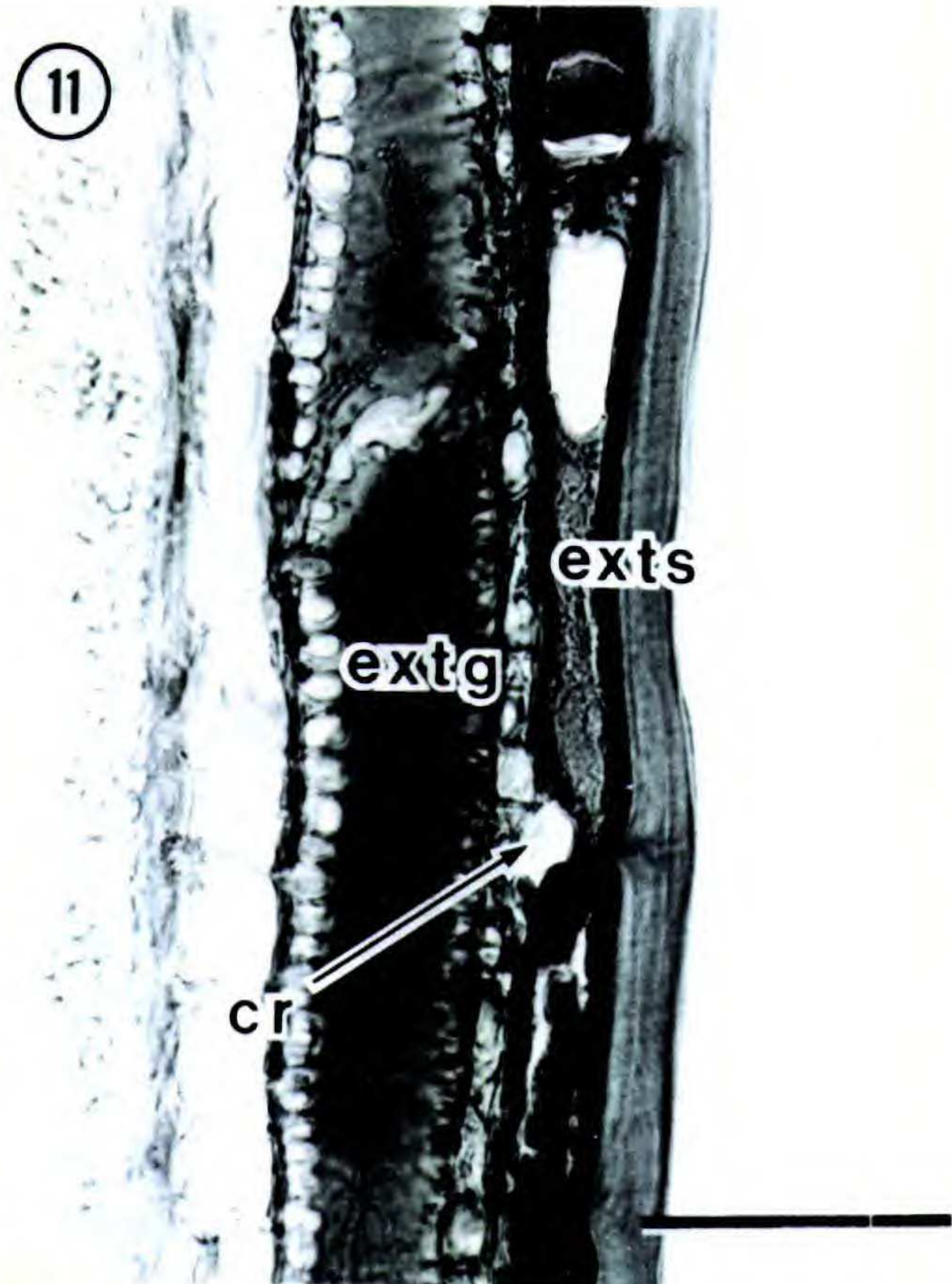
*Gynotroches*. The mature seeds of the only species of the genus, *G. axillaris*, are ellipsoid and small with an areolate surface (Fig. 18). They are

FIGURES 9–13.—9, 10. Mature arillate seed of *Crossostylis grandiflora* and longitudinal section (LS) of its seed coat.—11, 12. LS and transverse section of mature seed coat of *C. multiflora*.—13. LS of mature seed coat of *C. biflora*. Scales = 1 mm (Fig. 9) and 50  $\mu$ m (Figs. 10–13). exts, exotesta; rts, meso- and endotesta; extg, exotegmen; cr, crystal.

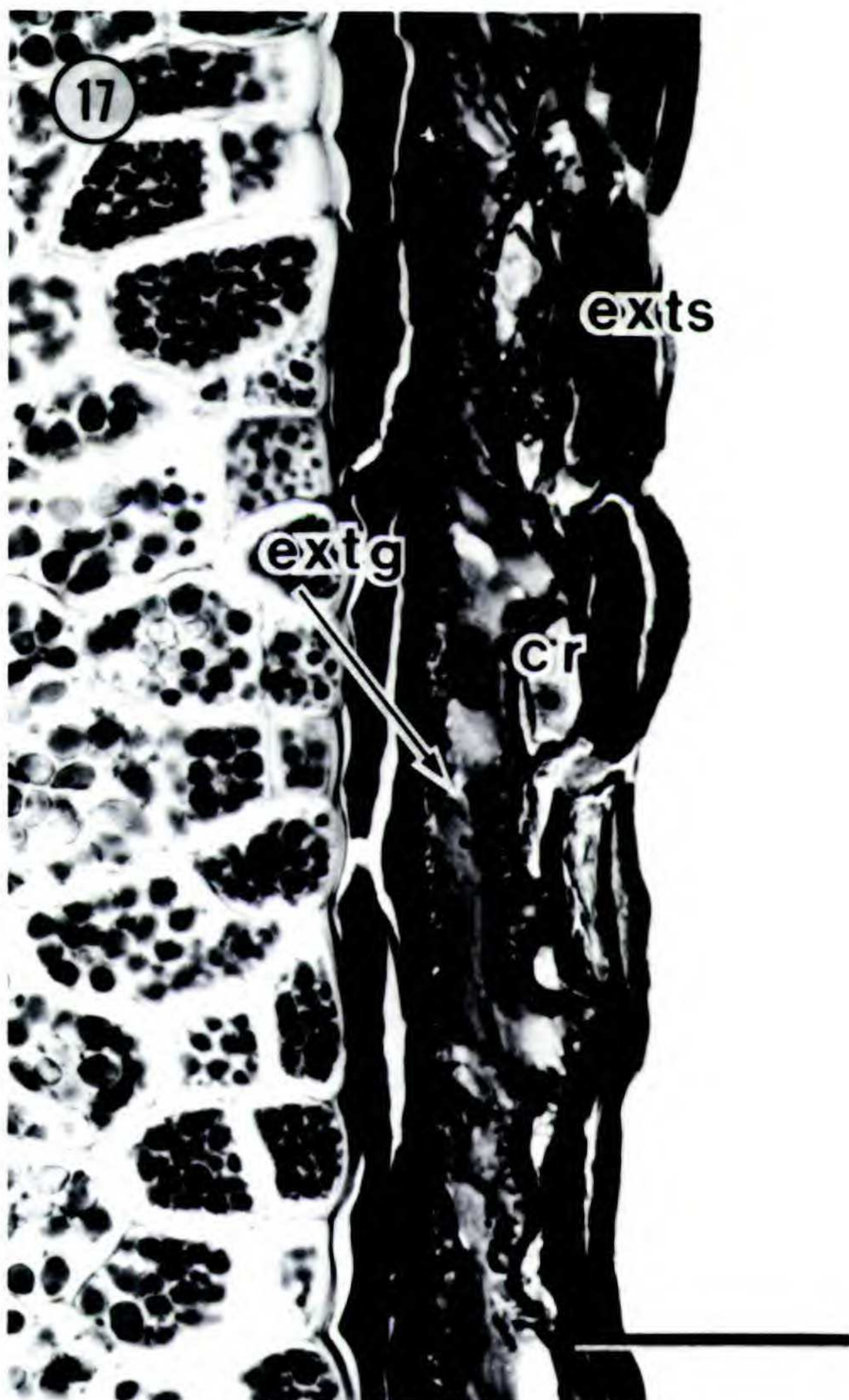
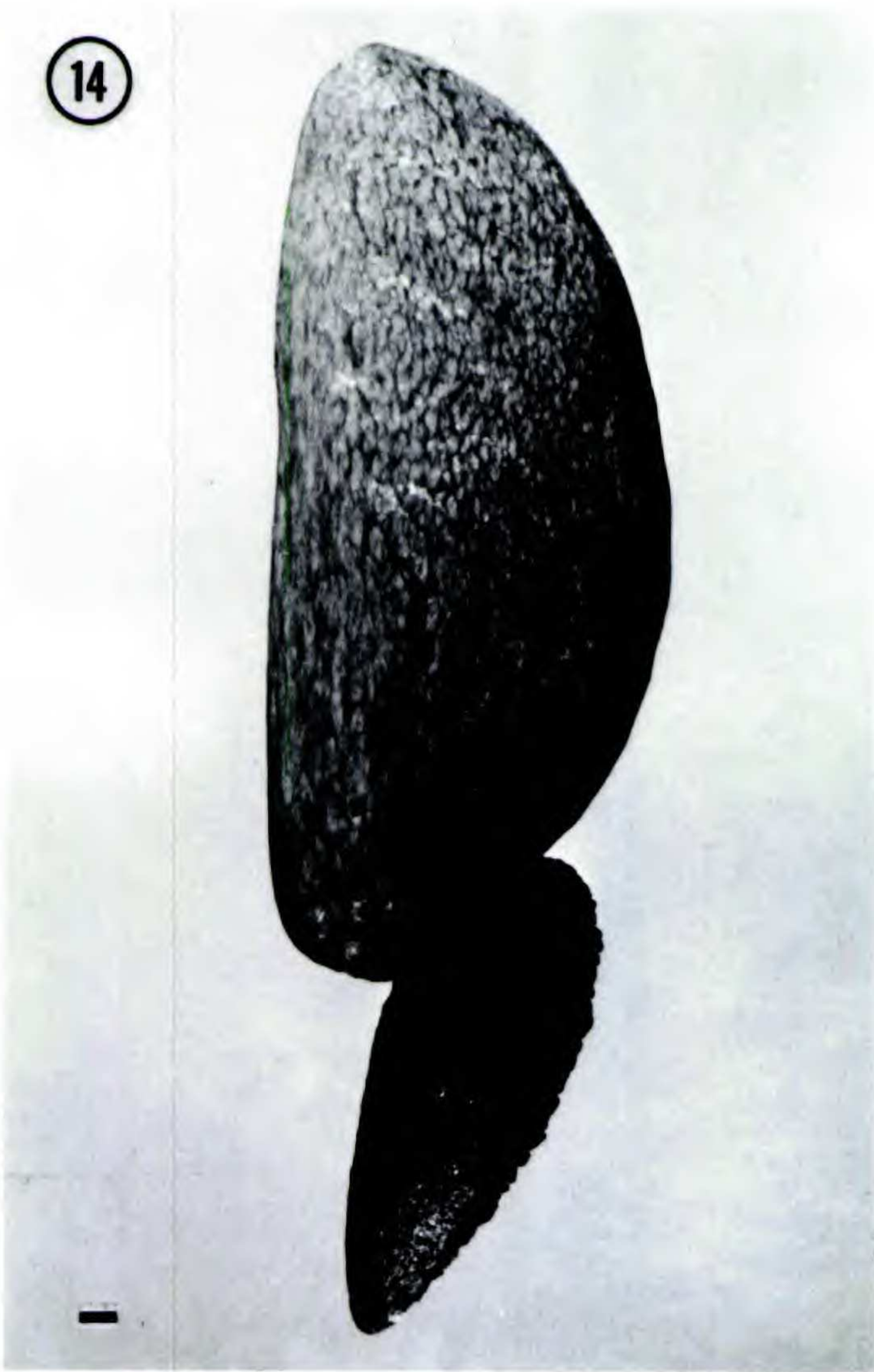
FIGURES 14–17.—14, 15. Mature winged seed of *Anopyxis klaineana* and longitudinal section (LS) of its seed coat.—16, 17. Mature winged seed of *Macarisia pyramidata* and LS of its seed coat. Scales = 1 mm (Figs. 14, 16) and 50  $\mu$ m (Figs. 15, 17). exts, exotesta; extg, exotegmen; cr, crystal.

FIGURES 18–21.—18, 19. Scanning electron micrograph (SEM) of mature nonappendaged seed of *Gynotroches axillaris* and longitudinal section (LS) of its seed coat.—20, 21. SEM of mature nonappendaged seed of *Pellacalyx cf. saccardianus* and LS of its seed coat. Scales = 200  $\mu$ m (Figs. 18, 20) and 50  $\mu$ m (Figs. 19, 21). exts, exotesta; ents, endotesta; extg, exotegmen; mtg, mesotegmen; entg, endotegmen.

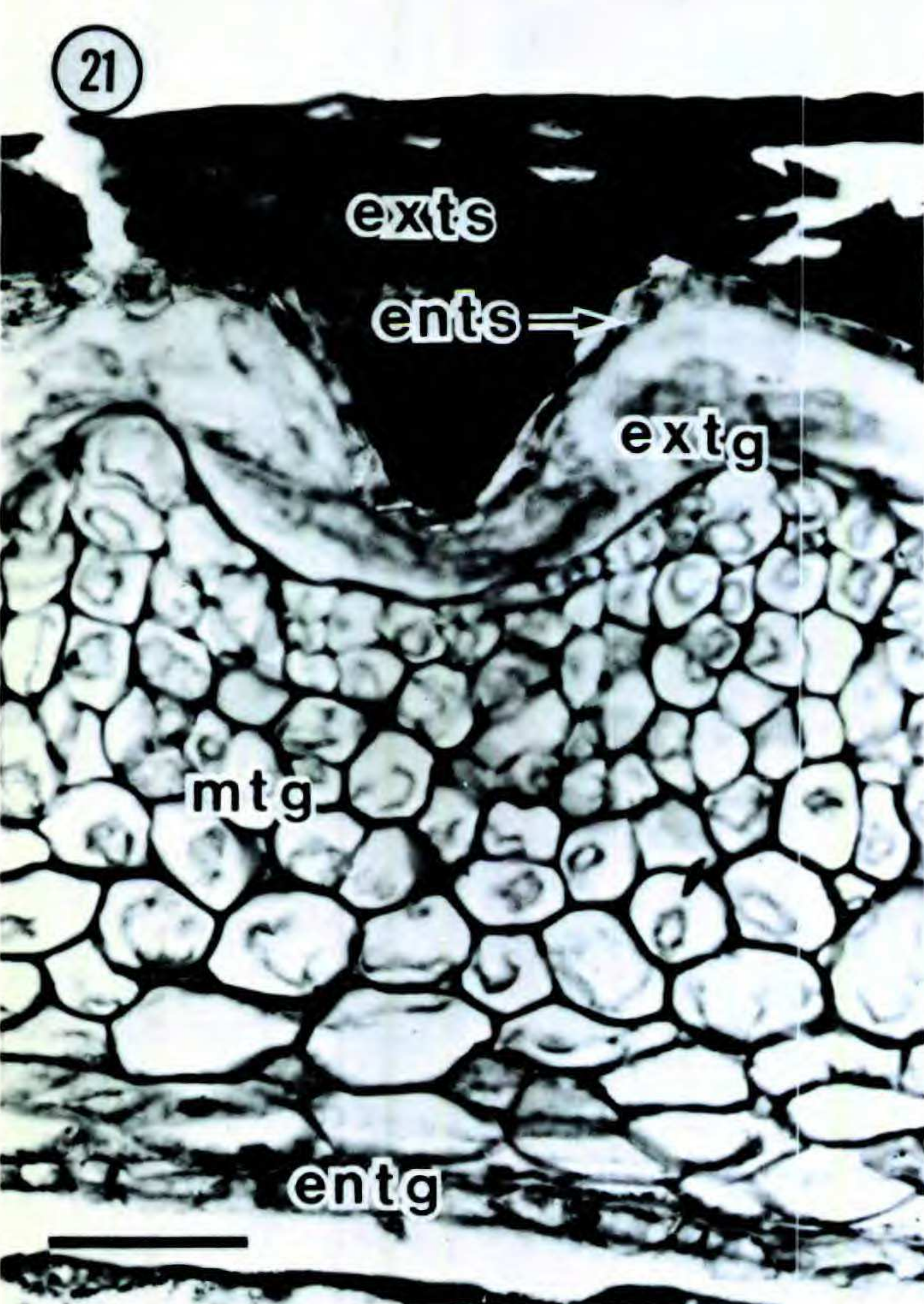
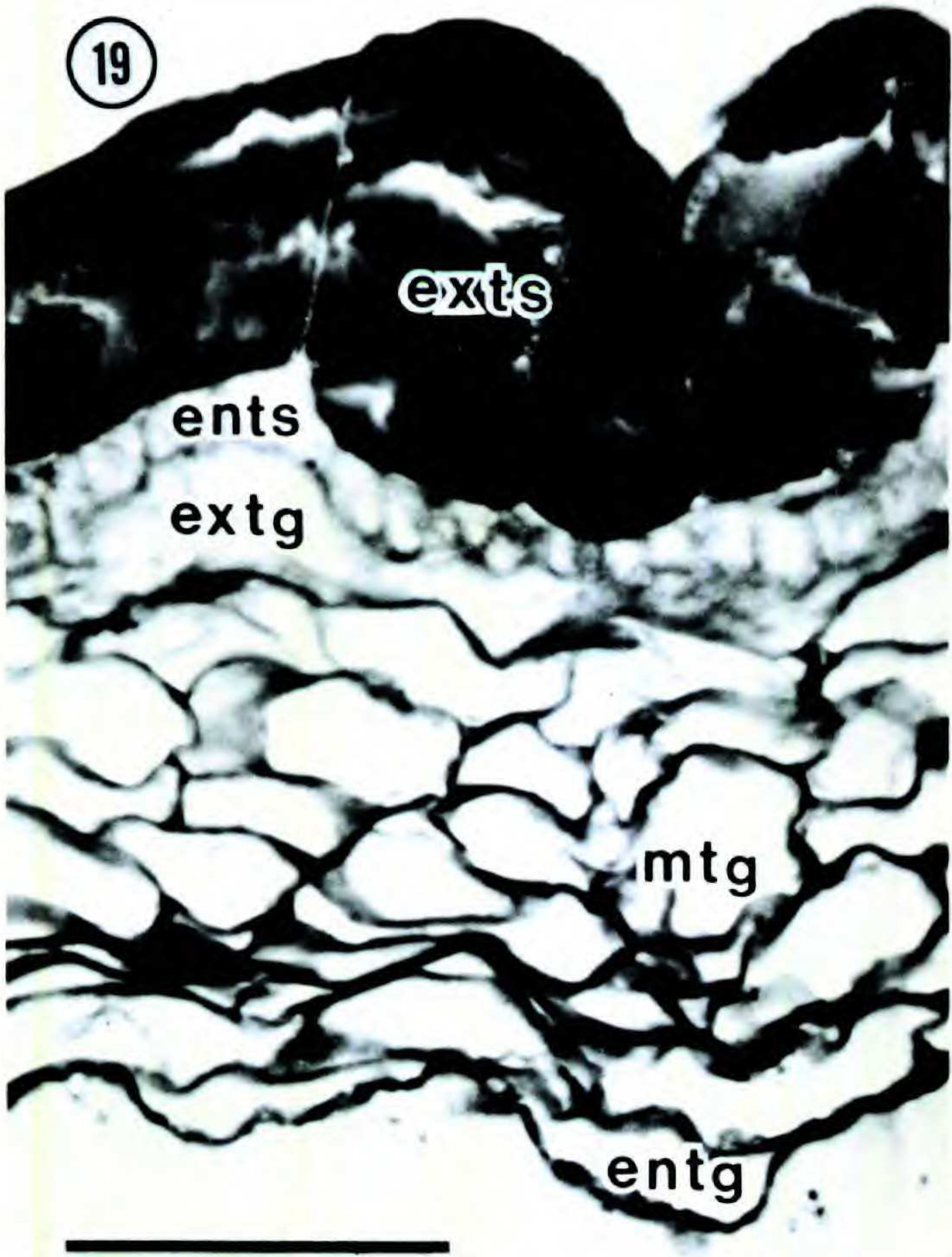




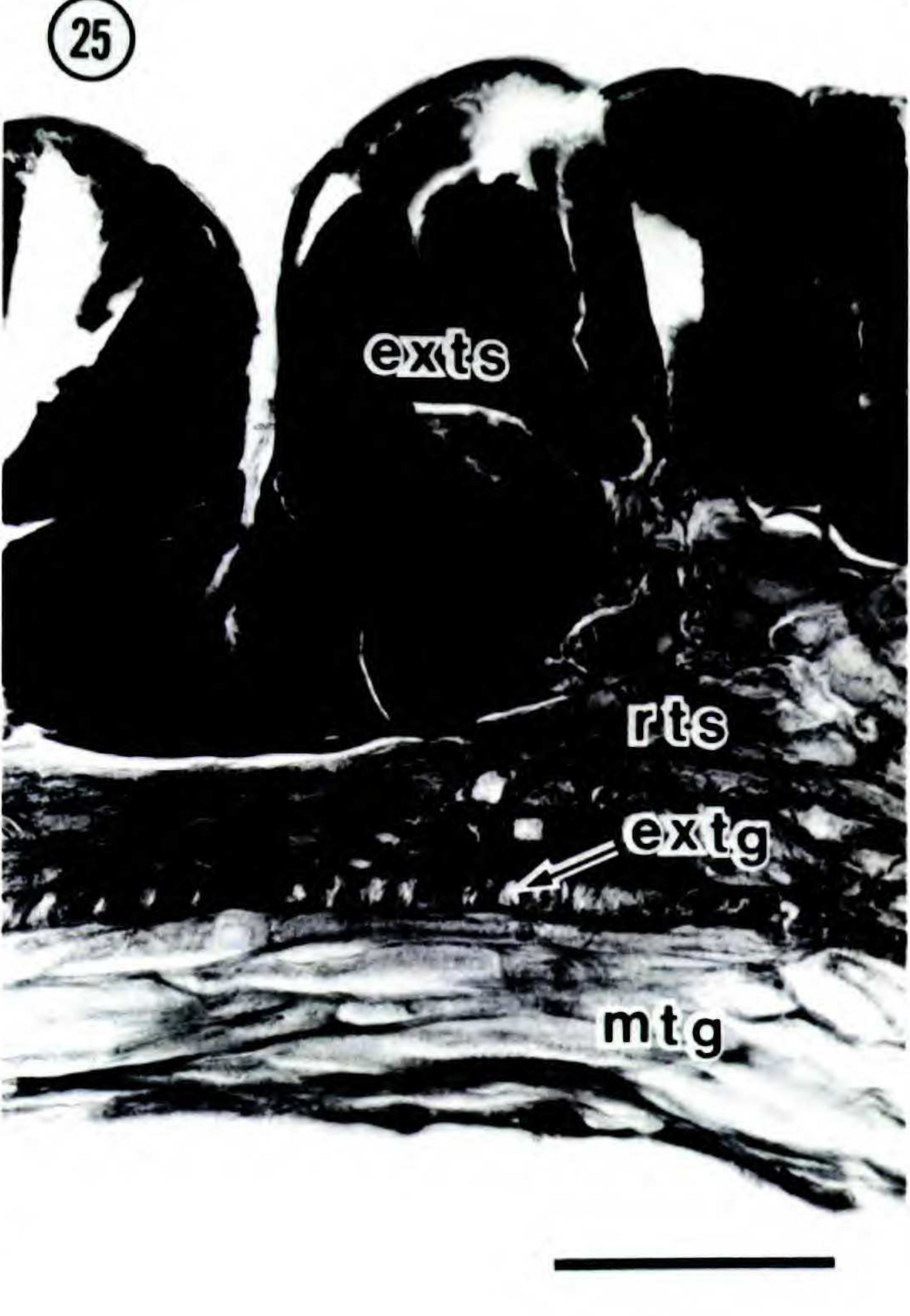
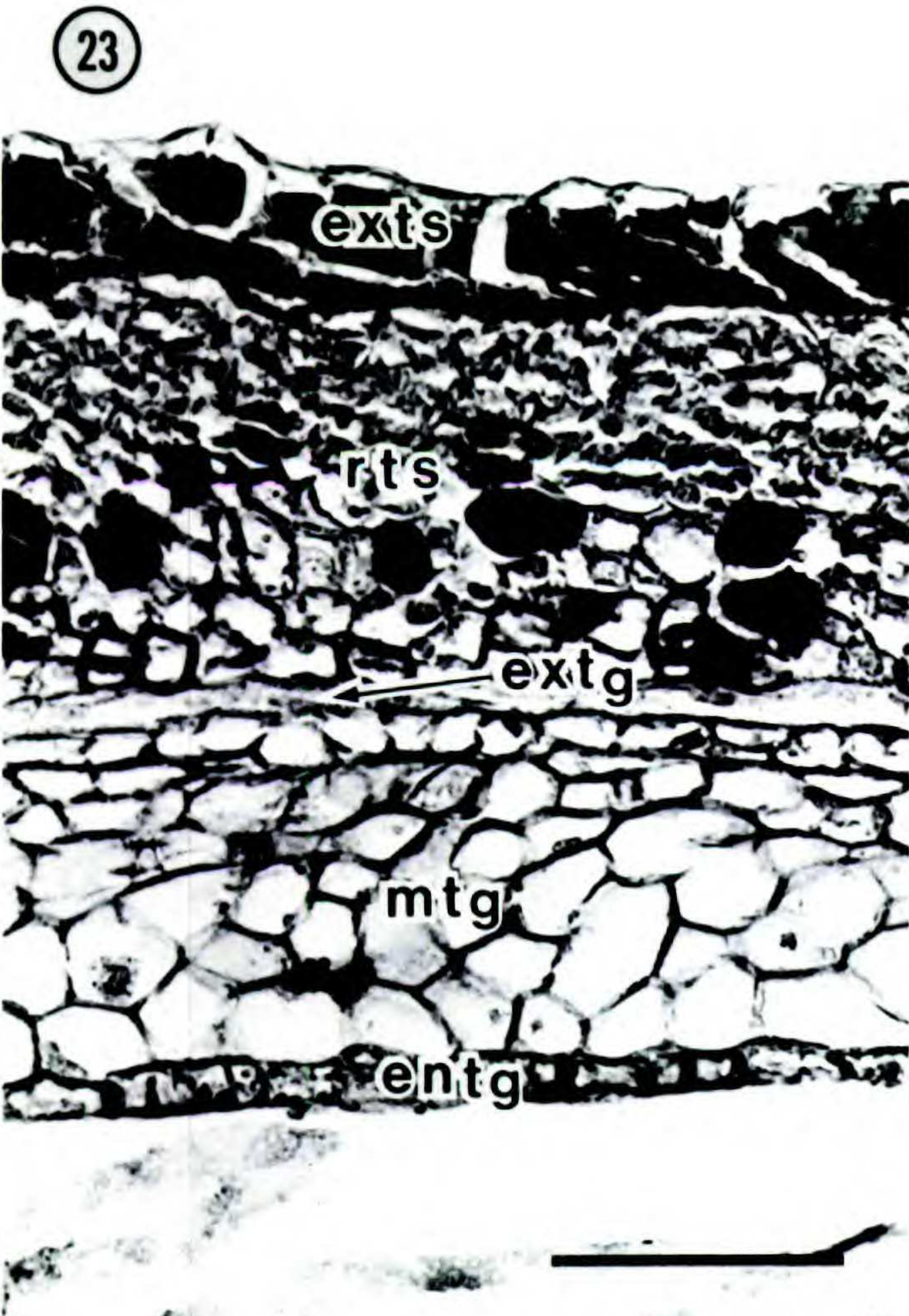
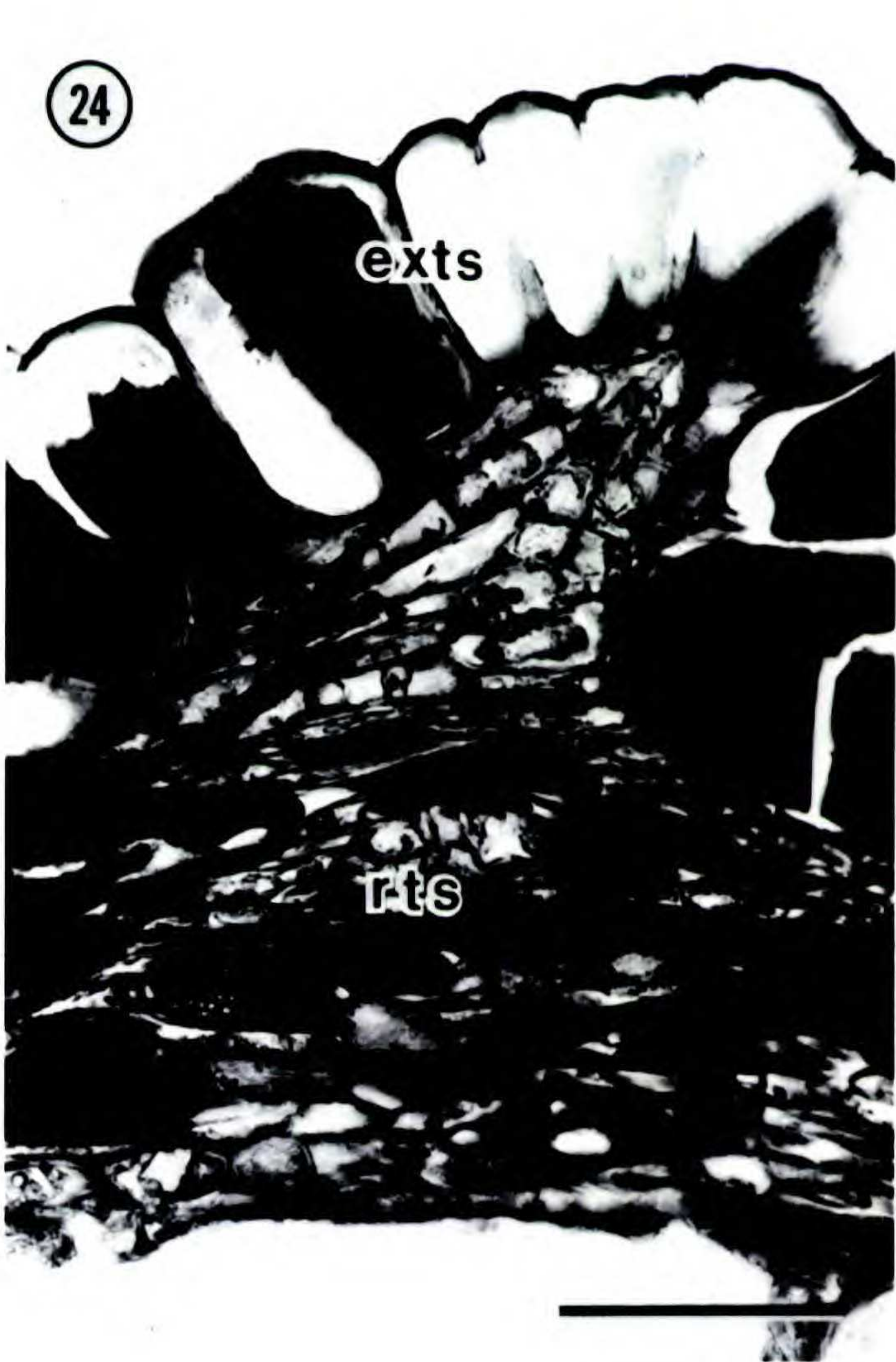
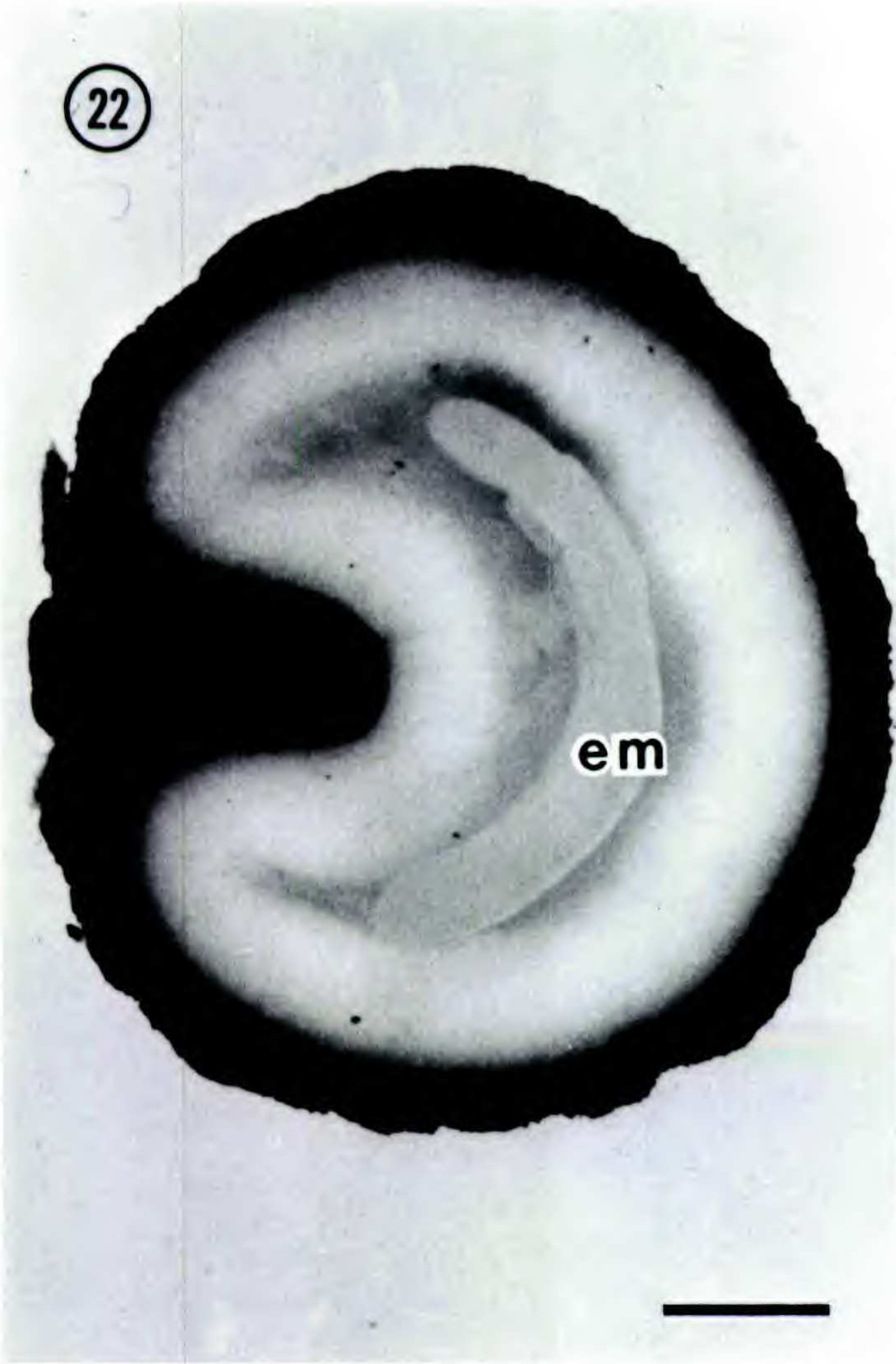














about 1.5 mm long and 0.5 mm thick (R-A) to 0.3 mm thick (L-L). A raphe is relatively conspicuous.

The mature seed coat is 0.12–0.14 mm thick and comprises a thick testa and a thick tegmen (Fig. 19). At the mature embryo sac stage, the outer and the inner integuments are 2 cells thick and 6–8 cells thick, respectively; a nonmultiplicative outer integument is characteristic of the genus. Even in the mature seed coat, all integumentary cell layers persist and form a 1-cell-layered exotesta, a 1-cell-layered endotesta, a 1-cell-layered exotegmen, a 4–6-cell-layered mesotegmen, and a 1-cell-layered endotegmen (Fig. 19). The exotesta is composed of remarkably enlarged, thick-walled, and tanniferous cells; the endotesta of much smaller and unspecialized cells; the exotegmen of radially elongate, thick-walled, fibrous cells; the underlying meso- and endotegmen of nonspecialized but somewhat thick-walled cells. Because of the very conspicuous development of the exotesta, the seed coat of *Gynotroches* is exotestal.

Corner (1976, 1: 161; 2: 260, fig. 315) reported that the mesotegmen (= “mesophyll”) is eventually crushed, and interpreted the cell layers below the exotegmen as the “nucellus.” However, since the nucellus disintegrates earlier, even in ovular stages (Juncosa, unpubl.), Corner seems to have misunderstood the persistent meso- and endotegmen as the “nucellus.”

*Pellacalyx*. The mature seeds of the genus are elliptic-oblong and small, often with an areolate surface. The shape and size of the mature seeds differ somewhat from species to species (Hou, 1958). The mature seed of *P. lobbii* and *P. cf. saccardianus* (Fig. 20) that were investigated in this study are both ellipsoid. Their size is 1.7–1.8 mm long and 0.7–1.1 mm in diameter in *P. lobbii* and 1.2–1.4 mm long and 0.7–0.8 mm in diameter in *P. cf. saccardianus*.

The mature seed coat of *Pellacalyx lobbii* and *P. cf. saccardianus* is nearly the same, 0.26–0.28 mm thick in total. The seed coat, like that of *Gynotroches*, is composed of a thick testa and a thick tegmen (Fig. 21). The outer and the inner integument are 2 cells thick and 6–8 cells thick, respectively; all cell layers persist up to the mature

seed coat stage, although the tegmen may further increase its thickness. Thus the mature seed coat comprises a 1-cell-layered exotesta, a 1-cell-layered endotesta, a 1-cell-layered exotegmen, a 6–9-cell-layered mesotegmen, and a 1-cell-layered endotegmen (Fig. 21). Exotestal cells are enlarged, thick-walled, and tanniferous; endotestal cells are much smaller and not specialized; cells of the exotegmen are longitudinally elongate, thick-walled, and fibrous; and those of the underlying meso- and endotegmen somewhat thick-walled. An undulation or “ribbon-like” structure (Corner, 1976) of the endotesta and the exotegmen is characteristic of the genus. As in the case of *Gynotroches*, Corner (1976, 1: 161, 2: 261, fig. 316) erroneously described the “nucellus” as persistent. But the nucellus that he considered is evidently the persistent meso- and endotegmen, because the nucellus completely disappears at a much earlier stage (Juncosa, unpubl.).

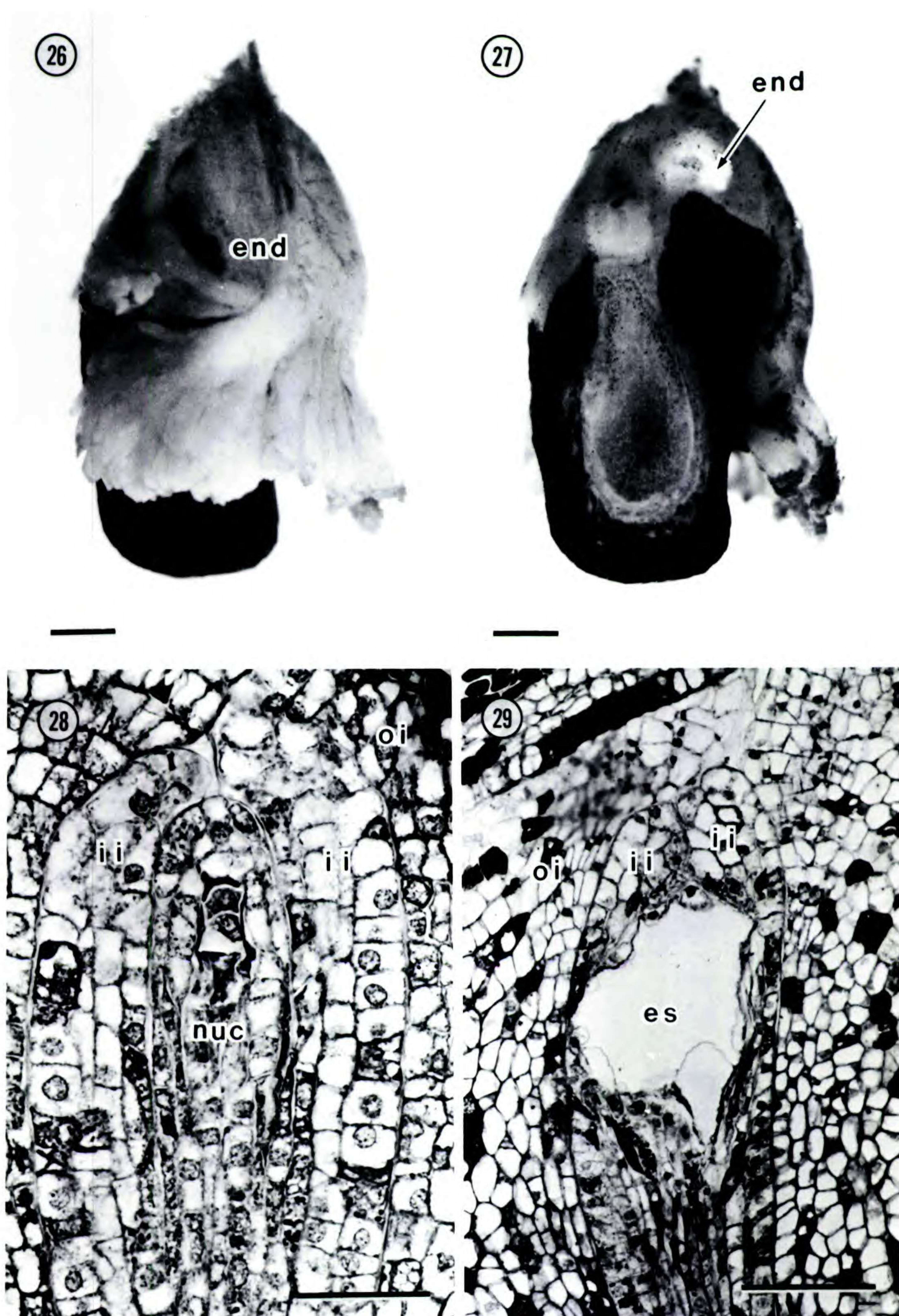
*Carallia*. The shape of the mature seed differs from species to species: oblong, oblong-ellipsoid, oblong-ovoid, ovoid, or reniform; the seed surface is areolate or corrugate; the size varies between 3 × 1.5 mm and 11 × 4 mm (Hou, 1958). The mature seeds examined of *C. brachiata* and *C. calophylloidea* are reniform, with the micropylar end close to the chalazal end and curved linear embryos (Fig. 22). The size is 5.5–6.0 mm long and 5.0–5.2 mm in diameter (when measured along the longest direction and the thickest middle part of the seed body). The mature seed of *C. eugenioidea*, another species investigated, is oblong-ovoid, and, probably like those of most other species, has a straight linear embryo; it is 3.0 mm long and 1.5 mm in diameter.

The mature seed coat of *Carallia brachiata* is 0.33–0.40 mm thick and is apparently composed only of a thick testa with exotestal cells extremely enlarged, thick-walled, and tanniferous (Fig. 24). Unlike the seed coat of *C. eugenioidea*, there is no tegmen, as Corner (1976) indicated. At the mature embryo sac stage, however, the outer and the inner integuments are 3–4 cells thick and 6–7 cells thick, respectively. Later, the young seed coat is evidently composed of a thicker testa and a thicker tegmen, where the differentiation of a

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FIGURES 22–25.—22. Longitudinal hand section of mature nonappendaged seed of *Carallia brachiata*.—23. Longitudinal section of young seed coat of *C. brachiata*.—24. Transverse section (TS) of mature seed coat of *C. brachiata*.—25. TS of mature seed coat of *C. eugenioidea*, with persistent tegmen. Scales = 1 mm (Fig. 22) and 100  $\mu$ m (Figs. 23–25). em, embryo; exts, exotesta; rts, meso- and endotesta; extg, exotegmen; mtg, mesotegmen; entg, endotegmen.





FIGURES 26-29. *Ceriops tagal*.—26. Mature seed covered with overflowing endosperm.—27. Longitudinal hand section of mature seed showing thick seed coat and endosperm.—28. Longitudinal section (LS) of a young ovule showing that both inner and outer integuments are multiplicative.—29. LS of a mature ovule with an



TABLE 2. Comparison in ovule, seed and fruit morphology, and putative methods of seed dispersal.

Tribe/Genus <sup>1</sup>	Ovules per Carpel <sup>2</sup>	Seeds per Fruit <sup>2</sup>	Seed Size	Seed Form	Fruit	Putative Methods of Seed Dispersal
Tribe Macarisieae						
<i>Blepharistemma</i>	2	6	medium	arillate	capsular	ants (birds?)
<i>Cassipourea</i>	2	(4-)6(-8)	medium	arillate	capsular	ants (birds?)
<i>Comiphyton</i>	2	1	medium	arillate	capsular	ants (birds?)
<i>Anopyxis</i>	2	10	medium	winged	capsular	wind
<i>Macarisia</i>	2	10	medium	winged	capsular	wind
<i>Sterigmapetalum</i>	2	10-12	medium	winged	capsular	wind
Tribe Gynotrocheae						
<i>Crossostylis</i>	2	several- many	small- medium	arillate	capsular	ants and/or birds
<i>Gynotroches</i>	many	many	small	nonappendaged	baccate	birds or mammals
<i>Pellacalyx</i>	many	many	small	nonappendaged	baccate	birds or mammals
<i>Carallia</i>	2	1(-5)	small- medium	nonappendaged	baccate	birds or mammals
Tribe Rhizophoreae						
<i>Bruguiera</i>	2	1	large	nonappendaged	indehiscent, hard-walled	sea water
<i>Ceriops</i>	2	1	large	nonappendaged	indehiscent, hard-walled	sea water
<i>Kandelia</i>	2	1	large	nonappendaged	indehiscent, hard-walled	sea water
<i>Rhizophora</i>	2	1	large	nonappendaged	indehiscent, hard-walled	sea water

<sup>1</sup> Tribal positions of genera follow Melchior (1964) and Floret (1976).

<sup>2</sup> Data from Alston (1925), Arènes (1954), Floret (1974, 1976), Geh & Keng (1974), Hou (1958, 1968), Sprague & Boodle (1909), Steyermark & Liesner (1983), Tomlinson et al. (1979), and our observations.

1-cell-layered exotegmen apparently occurs (Fig. 23). The structure of the exotegmen in the young seed coat in *C. brachiata* looks the same as those of other genera that have the persistent exotegmen. In *C. brachiata* the whole tegmen seems to degenerate as the seed develops. The meso- and endotesta, 10-20 cells thick in total, comprise much smaller cells than those of the exotesta.

The mature seed coat of *Carallia eugenioidea*, like that of *C. brachiata*, has a thick exotesta that comprises extremely enlarged, thick-walled, tanniferous cells (Fig. 25); the total thickness of the seed coat is 0.21-0.39 mm. The meso- and endotesta are histologically very similar and about 4-8 cell layers thick in total. Their cells may

contain crystals. *Carallia eugenioidea*, unlike *C. brachiata* but like *Gynotroches* and *Pellacalyx*, has a persistent tegmen, which comprises a 1-cell-layered fibrous exotegmen and a 4-5-cell-layered underlying mesotesta. The endotegmen appears to have nearly collapsed at maturity. At the mature embryo sac stage, the outer and the inner integument are only 3 cells thick and 5-6 cells thick, respectively. Therefore, even in postfertilization stages, nearly all cell layers of the inner integument appear to remain uncrushed.

Both *Carallia brachiata* and *C. eugenioidea* have no vascular bundles in the integuments or seed coats (except where a raphal vascular bundle is continued from a funicle). Because of the very

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organized embryo sac. The inner integument is being broken by an enlarging embryo sac. Scales = 1 mm (Figs. 26, 27), 50 μm (Fig. 28), and 100 μm (Fig. 29). end, endosperm; ii, inner integument; oi, outer integument; es, embryo sac; nuc, nucellus.



TABLE 3. Comparison in seed anatomy. Abbreviations: oi, outer integument; ii, inner integument; exts, exotesta; mts, mesotesta; ents, endotesta; extg, exotegmen; mtg, mesotegmen; entg, endotegmen; ts, testa. Seed coat categories follow Schmid (1986).

Tribe/Genus <sup>1</sup>	(Seed Form)	Thickness of Integuments <sup>2</sup> (Cell Layers)		Mature Seed Coat	
		oi	ii	Total Thickness (mm)	Composition
Tribe Macarisieae					
<i>Blepharistemma</i>	(arillate)	3–4	4–5	0.20–0.22	exts + mts + ents + extg (+ mtg?)
<i>Cassipourea</i>	(arillate)	3–6	5–8	0.16–0.22	exts + mts + ents + extg
<i>Comiphyton</i>	(arillate)	?	?	0.14–0.18	exts + mts + ents + extg
<i>Anopyxis</i>	(winged)	4–5	6–7	0.09–0.11	exts (+ mts + ents) + extg
<i>Macarisia</i>	(winged)	?	?	0.05–0.07	exts (+ ents) + extg
<i>Sterigmapetalum</i>	(winged)	2–4	8–10	0.08–0.10	exts + extg
Tribe Gynotrocheae					
<i>Crossostylis</i>	(arillate)	4–5	9–11	0.19–0.20 <sup>3</sup> 0.06–0.09 <sup>4</sup>	exts + mts + ents + extg <sup>3</sup> exts (+ mts + ents) + extg <sup>4</sup>
<i>Gynotroches</i>	(nonappendaged)	2	8	0.12–0.14	exts + ents + extg + mtg + entg
<i>Pellacalyx</i>	(nonappendaged)	2	6–8	0.26–0.28	exts + ents + extg + mtg + entg
<i>Carallia</i>	(nonappendaged)	3–4	5–7	0.21–0.40	exts + mts + ents (+ extg + mtg + entg) <sup>5</sup>
Tribe Rhizophoreae					
<i>Bruguiera</i>	(nonappendaged)	14–19	5–9	0.79–0.85	ts
<i>Ceriops</i>	(nonappendaged)	8–16	4–5	0.65–1.30	ts
<i>Kandelia</i>	(nonappendaged)	11–16	3–5	0.70–0.90	ts
<i>Rhizophora</i>	(nonappendaged)	13–18 <sup>6</sup>	4–6 <sup>6</sup>	0.60–1.00	ts

<sup>1</sup> Tribal positions of genera follow Melchior (1964) and Floret (1976).  
<sup>2</sup> In *Cassipourea* and *Sterigmapetalum*, inner and outer integuments are both initially two cells thick and later increase their thickness (Tobe & Raven, 1987a); this multiplicative nature of the integuments was further confirmed in *Blepharistemma*, *Ceriops*, and *Kandelia* in the present study and therefore is probably true of all other genera of Rhizophoraceae when they have thick integuments. Measurements of the thickness of the integuments were made on mature ovules with organized embryo sacs.  
<sup>3</sup> Data from *Crossostylis grandiflora*.  
<sup>4</sup> Data from *Crossostylis biflora* and *C. multiflora*.  
<sup>5</sup> In *Carallia* there appears to be a variation with respect to the seed coat structure and vasculature. See text for details.  
<sup>6</sup> Data from Carey (1934: 393, fig. 3).

conspicuous development of the exotesta as a mechanical structure, the seed coat of *Carallia* is exotestal.

NONAPPENDAGED VIVIPAROUS SEEDS

*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*. The mature seed taken from the indehiscent hard-walled fruit is cylindrical, 6.0–8.0 mm long, and 3.0–3.5 mm in diameter (*C. tagal*; Figs. 26, 27). The mature seed contains ample endosperm, as do those of the inland genera, but the endosperm of all the mangrove genera except *Bruguiera* characteristically extrudes from the micropyle and overflows the seed to fill up the space between the

fruit wall and the seed (Haberlandt, 1895; Cook, 1907; Carey, 1934; Juncosa, 1982, 1984b). Such an endosperm structure is most conspicuous in *Ceriops* (Figs. 26, 27), least so in *Kandelia*.

The mature seed coat anatomy does not show any diversity and is nearly the same in all four mangrove genera (Cook, 1907; Carey, 1934; Tobe, unpubl.). The mature seed coat is 0.6–1.3 mm thick in total and comprises only a thick testa; it completely lacks the tegmen. Although the massive inner integument is present at ovular stages (Fig. 28), it completely disintegrates in pre- and post-fertilization stages (Fig. 29; see also Cook, 1907; Carey, 1934). The testa is 20–60 cells thick but it is apparently undifferentiated and merely com-



TABLE 3. Continued.

Mature Seed Coat	Seed Coat	Endosperm
	Vasculature	Overflow
Category	Present (+) or Absent (-)	Sac (+) or Not (-)
exotestal	—	—
exotestal	—	—
exotestal	—	—
exotestal-exotegmic	—	—
exotestal-exotegmic	—	—
exotestal-exotegmic	—	—
exotestal <sup>3</sup>	—	—
exotestal-exotegmic <sup>4</sup>		
exotestal	—	—
exotestal	—	—
exotestal	— <sup>5</sup>	—
undifferentiated	+	+
undifferentiated	+	+
undifferentiated	+	+
undifferentiated	+	+

prises many tanniferous or nontanniferous cells and vascular tissues. According to Carey (1934), in *Rhizophora mucronata* “the outer integument [= testa] is differentiated into two zones, an outer which contains the extensive vascular supply, and an inner in which the cells are regularly arranged and meristematic,” but in *Ceriops candolleana* the inner one “is not sharply defined as it is in *Rhizophora*.” On the basis of our observations, the vascular strands, which are profusely branched in the testa, are distributed in the middle part of the testa in all the species examined, but they certainly do not always demarcate the inner zone. Since the seed coat anatomy of mangrove genera is not directly comparable with those of inland genera, it can be designated for our discussion as an “undifferentiated” seed coat.

DISCUSSION

As described above, the seeds of Rhizophoraceae show certain fundamental differences in their morphology and anatomy. These features are summarized in Tables 2 and 3. In Table 2, the methods

of seed dispersal are also indicated as a basis for subsequent discussions. Despite the diversity of these characters, there are several major character coincidences in certain groups of genera. All Macarisieae with a superior ovary (i.e., unspecialized ovary position), and *Crossostylis* (Gynotrocheae), with an inferior ovary (i.e., derived ovary position), always have either an aril or a wing on the seed; in contrast, the remaining genera, which have an inferior or semi-inferior ovary, lack any sort of seed appendage. Anatomically, all Macarisieae and Gynotrocheae (all inland groups) basically have a similar mature seed coat structure and consistently have a well-developed exotesta and (fibrous) exotegmen; their seed coat is either exotestal or exotestal-exotegmic. In contrast, all Rhizophoreae (the mangrove group) do not have a histologically differentiated seed coat, and they entirely lack a tegmen.

AFFINITIES OF RHIZOPHORAEAE

The accumulating data strongly confirm that Rhizophoraceae are monophyletic. In particular, the combination of subdermally initiated laticifers<sup>4</sup> in the gynoeclial wall (and sometimes even in other floral parts) with colletors<sup>5</sup> is unique to Rhizophoraceae (see also Juncosa & Tomlinson, this volume b). Dahlgren (this volume), on the basis of a cladistic approach incorporating various vegetative, reproductive (including embryological), and chemical characters, suggests that Rhizophoraceae are closely related to Elaeocarpaceae of Malvales and Celastraceae of Celastrales and possibly with Erythroxylaceae of Geraniales. We agree with this suggestion. In searching for closely related families, Dahlgren selected as plesiomorphies of Rhizopho-

<sup>4</sup> Juncosa & Tomlinson (1987) reported the presence of the subdermally initiated laticifers in mangrove genera; Floret (1974: 502, pl. 2, figs. a-c) figured this particular cell layer in the ovary wall of *Comiphyton gabonense*, although he did not specify it in the text. We confirmed the presence of laticifers in the ovary wall or calyx wall of *Gynotroches* (Gynotrocheae), *Anopyxis*, *Blepharistemma*, *Cassipourea*, and *Sterigmapetalum* (Macarisieae) but not in *Pellacalyx*. Material of *Macarisia* was not available to check this character.

<sup>5</sup> The occurrence of colleters has been recorded in *Cassipourea* (Alston, 1925), *Rhizophora* (Gill & Tomlinson, 1969; Lersten & Curtis, 1974), *Bruguiera* and *Kandelia* (Tomlinson et al., 1979; Metcalfe & Chalk, 1950, 1: 602; Hou, 1958). We confirmed the presence of colleters in all other genera available: *Carallia* (Gynotrocheae), *Blepharistemma*, *Macarisia*, and *Sterigmapetalum* (Macarisieae).



raceae the presence of an endothelium, the presence of an aril, the exotegmic seed coat, a chlorophyllous embryo, a Pvc-type sieve-element plastid, the presence of certain types of alkaloids, and the occurrence of a combination of some embryological features. We add the possession of deeply incised petals, because such petals are also undoubtedly plesiomorphic in Rhizophoraceae and Elaeocarpaceae. In addition, the occurrence of multiplicative inner and outer integuments may be more strongly emphasized as another symplesiomorphy shared by all of the families mentioned above.

From the viewpoint of seed morphology and anatomy, *Blepharistemma*, *Cassipourea*, and *Comiphyton* of Macarisieae best agree with Elaeocarpaceae and Celastraceae in having arillate seeds and a fibrous exotegmen (and albuminous seeds and linear embryos; Weibel, 1968; Corner, 1976). The only conspicuous difference between these three genera of Macarisieae and Elaeocarpaceae–Celastraceae is the absence of a persistent meso- and/or endotegmen in the latter. In Rhizophoraceae, a persistent meso- and endotegmen occurs only in *Gynotroches*, *Pellacalyx*, and certain species of *Carallia*, all of which are undoubtedly specialized genera in the family as discussed later. Seed morphology and anatomy have not been investigated fully in Elaeocarpaceae and Celastraceae, and therefore it cannot be determined with certainty that this difference will hold up when more information is available. Critical, however, is the fact that the arillate seeds occur in the genera of Macarisieae that have a superior ovary (a plesiomorphy), and that a fibrous exotegmen is common to all inland genera, which are less advanced in general than the mangrove genera. These features support Dahlgren's suggestion that the presence of an aril and a fibrous exotegmen is plesiomorphic in Rhizophoraceae and justify the use of those seed features in searching for related families.

Comparisons with Anisophylleaceae may also be needed. Even though embryological evidence as well as various other lines of evidence suggest that this family is distinct (Tobe & Raven, 1987b), wood anatomy (Keating & Randrianasolo, this volume; Baas, pers. comm.), and floral morphology (Tobe & Raven, in press) link it with Rhizophoraceae. Wood and leaf anatomy particularly suggest that Anisophylleaceae and Gynotrocheae may be closely related. Our observations, however, indicate that Anisophylleaceae lack subdermally initiated laticifers and colleters, both of which are characteristic of Rhizophoraceae and support their interpretation as a closely linked monophyletic evolutionary unit

not directly related to Anisophylleaceae. The present study further shows that, even apart from the presence or absence of an aril, the seed morphology and anatomy of Anisophylleaceae differ greatly from those of Rhizophoraceae in completely lacking a tegmen (see Tobe & Raven, 1987b, for data on Anisophylleaceae). Therefore, Anisophylleaceae seem clearly to be much more distantly related to Rhizophoraceae than to Elaeocarpaceae and Celastraceae; Rhizophoraceae and Anisophylleaceae are evidently more distantly related than we have suggested elsewhere (Tobe & Raven, in press).

Dahlgren (this volume) has suggested that Elaeocarpaceae have probably been misplaced in Malvales and ought to be transferred near Celastraceae of Celastrales sensu Dahlgren, along with Rhizophoraceae. In terms of seed coat anatomy, most Malvales other than Elaeocarpaceae (e.g., Bombacaceae, Malvaceae, Sterculiaceae, and Tiliaceae) are characterized by a palisadal structure of exotegmen, which is unknown in Elaeocarpaceae (see Corner, 1976). Thus the seed coat anatomy also supports the exclusion of Elaeocarpaceae from Malvales and, as already discussed above, their close relationships with Rhizophoraceae and Celastraceae.

#### EVOLUTION OF SEEDS IN RHIZOPHORACEAE

As discussed above, the arillate seeds of *Blepharistemma*, *Cassipourea*, and *Comiphyton* (Macarisieae) and *Crossostylis* (Gynotrocheae) apparently represent an archaic, ancestral state in Rhizophoraceae. Judged from the distribution of seed characters in Rhizophoraceae (Tables 2, 3), some of the specialized seed types seem clearly to have evolved more than once.

In Macarisieae, arillate seeds (in *Blepharistemma*, *Cassipourea*, and *Comiphyton*) and winged seeds (in *Anopyxis*, *Macarisia*, and *Sterigma-petalum*), both types borne in capsular fruits, are probably dispersed by ants and wind, respectively; arillate seeds might also be dispersed by birds (see Ridley, 1930; van der Pijl, 1969, for general discussions of seed dispersal). What may have induced an evolutionary change from ant dispersal to wind dispersal is uncertain. Anatomically, in contrast with a relatively thick seed coat of arillate seeds (ca. 0.2 mm thick), the seed coat of winged seeds is thinner (less than 0.1 mm thick). The thinner seed coat might be adaptive in lightening the seeds for wind dispersal. Despite this innovation in seed dispersal, however, the area of distribution of the genera with winged seeds is at present restricted. *Anopyxis* is restricted to West Africa, *Macarisia*



to Madagascar, and *Sterigmapetalum* to the Amazon (see Juncosa & Tomlinson, this volume b, for a distribution map). In contrast, *Cassipourea*, which has arillate seeds, is widely distributed in Africa, India, and South America. *Blepharistemma* and *Comiphyton*, also with arillate seeds, are confined to the Kerela district of southwestern India and West Africa, respectively.

The seeds of *Crossostylis*, which traditionally has been assigned to Gynotrocheae, resemble those of *Blepharistemma*, *Cassipourea*, and *Comiphyton* in having an aril and in being produced in capsular fruits. The distribution of *Crossostylis* (comprising 13 species) at present is restricted to and scattered in Polynesian islands, considerably separated from that of Macarisieae; it partly overlaps with the distribution area of the rest of Gynotrocheae and of Rhizophoreae. These facts may suggest that the arillate, small-medium-sized seeds of *Crossostylis* are now or formerly were dispersed by birds from one island to another. Ridley (1930: 423–424) discussed bird-dispersed arillate seeds. Van der Pijl (1969: 30) gives an example: in Indonesia, the fruit-pigeons (*Carpophaga*) eat nutmeg with its aril (“arillode”) and disseminate it outside the region. Variation in seed size and seed coat anatomy within the genus may reflect complex methods of seed dispersal.

The nonappendaged seeds of *Carallia*, *Gynotroches*, and *Pellacalyx* (Gynotrocheae), which are borne in baccate fruits, are much smaller than the arillate seeds of Macarisieae in general. The number of seeds per fruit is either 1(–5) (*Carallia*) or ca. 20–40 (*Gynotroches* and *Pellacalyx*). Those seeds are very hard and were difficult to section with a microtome. Fruit and seed structure of these genera seem to indicate that the seeds are endozoochorous and dispersed by birds or mammals. Bird or bat dispersal seems to provide a likely explanation of the wide distribution of these genera throughout the islands of southeastern Asia, west to India and Madagascar (*Carallia*).

Seeds of the four mangrove genera—*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora* of Rhizophoreae—produce viviparous seedlings in indehiscent hard-walled fruits. They do not exhibit histological differentiation in their seed coats, probably because the seeds are protected by the fruit wall and therefore are not specialized against external environments. When they fall from the parent plant, the dropped fruits or seedlings are undoubtedly dispersed by sea water, as discussed by many workers (e.g., Ridley, 1930; Hou, 1958). The mangrove genera are at present best represented from the western Pacific to the Indian Ocean; *Rhizophora*

is pantropical (Graham, 1964). *Rhizophora*, the most widely distributed genus of the family, is also the only one that is wind pollinated (Tomlinson et al., 1979), a system that might be well suited to newly colonized habitats.

To sum up, the seeds of Rhizophoraceae seem to have evolved as the result of adaptation to changes in seed dispersal methods, that is, from ant dispersal to dispersal by wind, bird, mammal or water. The diversity in the seed morphology and anatomy, in conjunction with the diversity of fruit structure, is well explained by such changes in the methods of seed dispersal, and vice versa. However, the actual methods of dispersal of the seeds of the nonmangrove genera are very poorly known and should be studied in the field.

#### PHYLOGENETIC RELATIONSHIPS WITHIN RHIZOPHORACEAE

The accepted infrafamilial classification of Rhizophoraceae is based primarily on androecial position (i.e., perigynous or epigynous), the number of carpels or ovarian locules, and the number of ovules per carpel (e.g., Melchior, 1964). Data from seed morphology and anatomy and fruit structure generally support the traditional classification in separating Macarisieae, Gynotrocheae, and Rhizophoraceae as distinct units.

For the cladistic analysis, we chose 16 characters whose character-state evaluations were possible; these include characters of embryology, seed morphology and anatomy, and floral morphology (Table 4). The character-state evaluation in Rhizophoraceae was made on the basis of outgroup comparison with Elaeocarpaceae and/or Celastraceae. Data on Rhizophoraceae, Elaeocarpaceae, and Celastraceae were obtained from the following references: Rhizophoraceae—Schimper (1893), Haberlandt (1895), Cook (1907), Carey (1934), Melchior (1964), Floret (1974, 1976), Corner (1976), Tomlinson et al. (1979), Juncosa (1982, 1984a, b), Tobe & Raven (1987a), and present study; Elaeocarpaceae—Mauritzon (1934), Venkata Rao (1953), Corner (1976), Cronquist (1981), and Hyland & Coode (1982); Celastraceae—Mauritzon (1936), Berkeley (1953), Adatia & Gavde (1962), Copeland (1966), Corner (1976), and Cronquist (1981). Results of character-state evaluation within the Rhizophoraceae are provided in Table 4, their distribution in the family in Table 5, and a cladogram based on these features in Fig. 30.

The cladogram (Fig. 30) indicates that, except for six genera of Macarisieae, the eight remaining



TABLE 4. Character-state evaluation of some selected reproductive characters in Rhizophoraceae.

Character	Plesiomorphy <sup>1</sup>	Apomorphy
1. Ovary position	superior	inferior or semi-inferior
2. Numbers of ovules per carpel	2	many
3. Structure of nucellus	crassinucellate	tenuinucellate
4. Number of archesporial cells in ovule	many	1
5. Formation of endothelium	occurs	absent
6. Nature of outer integument	multiplicative	not multiplicative
7. Integumentary (or seed coat) vasculature	absent	present
8. Development of endosperm	not overflow from embryo sac	overflow
9. Seedling	not viviparous	viviparous
10. Fruit morphology	capsular	baccate or indehiscent
11. Type of seed appendage	aril	wing
12. Presence or absence of seed appendage	present	absent
13. Total thickness of mature seed coat	> 0.1 mm	< 0.1 mm
14. Histological differentiation of seed coat	occurs	does not occur
15. Development of exotegmen	persistent, fibrous	early disintegration
16. Development of meso- and endotegmen	early disintegration	persistent

<sup>1</sup> All plesiomorphies occur not only in some or all inland genera of Rhizophoraceae but also are common to the outgroups, e.g., Elaeocarpaceae and Celastraceae. References for data on each family are presented in the text.

genera of the family share an inferior or semi-inferior ovary (a synapomorphy). The genera of Macarisieae retain many plesiomorphic features, including a superior ovary. Within Macarisieae, Floret (1976) recognized three subgroups on the basis of floral and seed characters: 1) *Anopyxis*, *Macarisia*, and *Sterigmapetalum*; 2) *Blepharistemma*, *Comiphyton*, and *Cassipourea* subg.

*Dactylopetalum*; and 3) the three remaining subgenera of *Cassipourea* (see Tobe & Raven, 1987a, for revision). Later, emphasizing probable coincidences in the seed morphology and anatomy, but on the basis of meager data, we suggested closer affinities among *Anopyxis*, *Macarisia*, and *Sterigmapetalum* on the one hand, and among *Blepharistemma*, *Cassipourea*, and *Comiphyton*

TABLE 5. Distribution of character states of some selected reproductive characters in Rhizophoraceae. Plesiomorphy (-); Apomorphy (+). Character numbers correspond to those given in Table 4.

Genus	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Blepharistemma</i> (BLE) <sup>1</sup>	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cassipourea</i> (CAS)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Comiphyton</i> (COM)	-	-	-	?	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anopyxis</i> (ANO)	-	-	-	?	-	-	-	-	-	-	+	-	+	-	-	-
<i>Macarisia</i> (MAC)	-	-	-	?	-	-	-	-	-	-	+	-	+	-	-	-
<i>Sterigmapetalum</i> (STR)	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-
<i>Crossostylis</i> (CRS)	+	-	-	- <sup>2</sup>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gynotroches</i> (GYN)	+	+	+	+	-	+	-	-	-	+		+	-	-	-	+
<i>Pellacalyx</i> (PEL)	+	+	+	+	-	+	-	-	-	+		+	-	-	-	+
<i>Carallia</i> (CAR)	+	-	-	+	-	-	-	-	-	+		+	-	-	-	+
<i>Bruguiera</i> (BRU)	+	-	-	?	+	-	+	+	+	+		+	-	+	+	-
<i>Ceriops</i> (CER)	+	-	-	- <sup>3</sup>	+	-	+	+	+	+		+	-	+	+	-
<i>Kandelia</i> (KAN)	+	-	-	?	+	-	+	+	+	+		+	-	+	+	-
<i>Rhizophora</i> (RHZ)	+	-	-	?	+	-	+	+	+	+		+	-	+	+	-

<sup>1</sup> Three-letter abbreviations given in parentheses are used in a cladogram (Fig. 30).

<sup>2</sup> Data from personal observations on *Crossostylis grandiflora*.

<sup>3</sup> The number of archesporial cells in an ovule in the mangrove genera is not well documented; Karsten (1891) described two megaspore mother cells in *Ceriops candolleana*. This character must be confirmed in this and other mangrove genera.



on the other (Tobe & Raven, 1987a). The present study confirms the relationships that we suggested then. Character-state comparisons indicate that *Anopyxis*, *Macarisia*, and *Sterigma-petalum* share the synapomorphies winged seeds and a thinner seed coat, and thus constitute a single clade. On the basis of seed morphology and anatomy, therefore, we propose the division of Macarisieae into two subtribes: 1) Cassipourinae, comprising *Blepharistemma*, *Cassipourea*, and *Comiphyton*; and 2) Macarisinae, comprising *Anopyxis*, *Macarisia*, and *Sterigma-petalum*. Wood anatomy (van Vliet, 1976) and leaf architecture (Keating & Randrianasolo, this volume) do not provide a clear distinction between the two subtribes; wood anatomical comparison rather suggests that *Comi-phyton* is intermediate between *Macarisia* (Ma-carisinae) and *Cassipourea* (Cassipourinae) (van Vliet, 1976). An overall comparison of their veg-etative morphology (Sprague & Boodle, 1909), however, suggests close affinities between *Ano-pyxis* and *Macarisia*. Leaf anatomy strongly sup-ports our suggested subtribal classification (Baas, pers. comm.): *Anopyxis*–*Macarisia*(–*Sterigma-petalum*) have a nonpluriseriate epidermis and a differential hypodermis, whereas *Blepharistem-ma*–*Cassipourea*(–*Comiphyton*) have a plurise-riate epidermis but lack a discernible hypodermis. For further elucidation of the relationships in this group, a comprehensive study of the largest and most widely distributed genus, *Cassipourea*, seems essential.

*Crossostylis*, which has been placed in Gyno-trocheae, shares only one apomorphy (an inferior ovary) with any group other than the six genera of Macarisieae. Apart from the ovary position, in contrast, *Crossostylis* agrees nearly completely with Macarisieae in many plesiomorphic features. Juncosa & Tomlinson (this volume b) summarize that *Crossostylis* shares stilt roots, roots having no hairs, bijugate phyllotaxy, imbricate stipules, flat floral apices, and several-layered laticifers with other Gynotrocheae (sometimes excepting *Pellacalyx*), and shares most of these features also with Rhi-zophoreae. It is uncertain whether those shared structures represent apomorphic character states or not, but at least some of them are probably synapomorphies, suggesting phylogenetic affinities of *Crossostylis* with the rest of Gynotrocheae and all Rhizophoreae.

*Crossostylis*, however, is clearly distinguished from other Gynotrocheae and all Rhizophoreae in not sharing the apomorphies noncapsular fruit and the nonappendaged seed. The cladistic analysis thus indicates mutual closer affinities between the rest

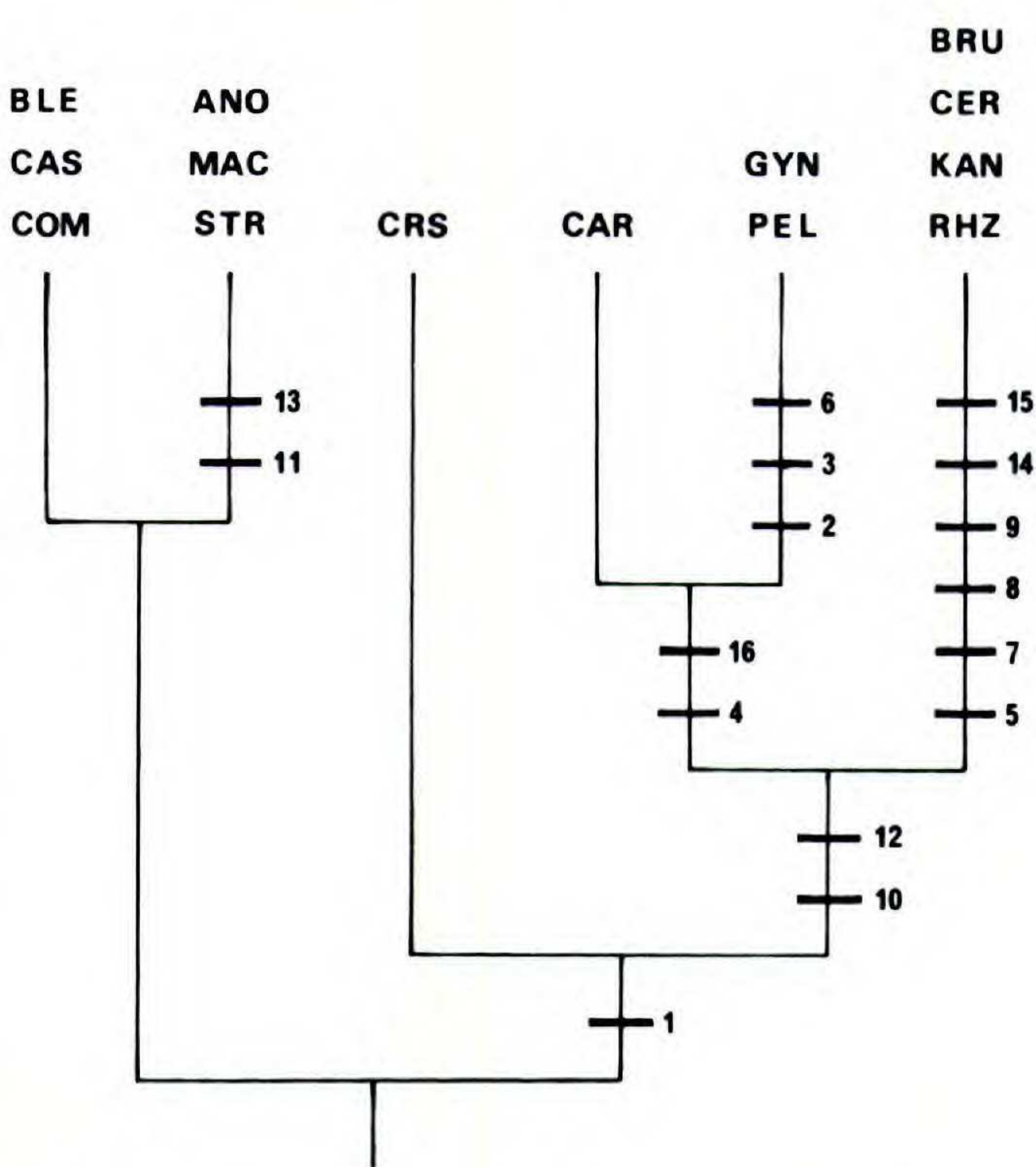


FIGURE 30. A cladogram illustrating evolutionary interrelationships of the genera of Rhizophoraceae. Character numbers 1–16 and three-letter abbreviations of genera are shown in Tables 4 and 5, respectively.

of Gynotrocheae and all Rhizophoreae, and leaves *Crossostylis* in a distinct evolutionary line. Juncosa (unpubl.) suggests an intermediate position for *Crossostylis* between Macarisieae and Gynotro-cheae, and we agree with this interpretation. *Cros-sostylis* seems to be more appropriately assigned to its own tribe, Crossostylideae, as also suggested by Juncosa (pers. comm.).

*Carallia*, *Gynotroches*, and *Pellacalyx* have been grouped in Gynotrocheae; this treatment seems reasonable because as a group they have no syn-apomorphies with Rhizophoreae. The three genera share two synapomorphies: a one-celled ovuled ar-chesporium and a persistent meso- and endotegmen (although the latter feature may be inconsistent in *Carallia*). *Gynotroches* and *Pellacalyx* closely re-semble each other in sharing the following addi-tional apomorphies: a multiovulate carpel, a tenuinucellate ovule, and a nonmultiplicative outer integument; in contrast, *Carallia* is characterized by retaining the plesiomorphic states of those char-acters. Thus, we suggest that *Gynotroches* and *Pellacalyx* should be segregated as a subtribe Gy-notrochinae, and *Carallia* should be treated as the monogeneric subtribe Carallinae.

In considering the phylogenetic relationships of *Carallia*, the diversity within the genus must be taken into account. For example, with respect to the mature seed coat structure, Corner (1976) described “tegmen without trace” in *Carallia*



*brachiata*; likewise, Juncosa (unpubl.) did not see a tegmen in *C. borneensis*. We did not observe a tegmen in the mature seed coat of *C. brachiata*, either (Fig. 24). In contrast, in the mature seed coat of *C. eugenioidea* (Fig. 25) and in the younger seed coat of *C. brachiata* (Fig. 23), we observed thick, distinct tegmic cell layers, the outermost of which even assumed the fibrous, exotegmenlike structure that is characteristic of all other inland genera. In its lack of a tegmen in the mature seed coat, *Carallia* might be compared to Rhizophoreae; however, when they are compared throughout their ontogeny, they appear to be quite distinct. Thus, in Rhizophoreae, the inner integument or young tegmen soon disintegrates because of the enlargement of the embryo sac in postfertilization stages, but in *Carallia* it does not disintegrate until much later, and it may even persist, as in *C. eugenioidea*. Furthermore, in *Carallia* the outermost cell layer of the inner integument differentiates into the fibrous exotegmen, but in Rhizophoreae such a histological differentiation has not been observed.

The thickness and vasculature of the outer integument in *Carallia* seems to be diverse. According to Juncosa (unpubl.), *C. borneensis* has a 7–15-cell-layered outer integument at anthesis, which is vascularized as it is in Rhizophoreae. However, in the samples of *C. brachiata* and *C. eugenioidea* we observed, there were only 3–4-cell-layered outer integuments at the mature embryo sac stage; the outer integument of those two species has not space for vascularization at that stage, and no vascular bundles were observed in testae even in later stages, although the raphe always contained some vascular tissues.

To sum up, we suggest that in *Carallia*, as well as in *Gynotroches* and *Pellacalyx*, the tegmen was originally persistent, but that a tegmenless seed coat (as in *C. brachiata* and *C. borneensis*) apparently evolved, almost certainly independently from Rhizophoreae. Likewise, the vasculature of the testa in *Carallia* seems to have been acquired only in certain species of the genus with an extremely thickened outer integument or testa, but probably independently of the evolutionary line leading to Rhizophoreae.

Although *Carallia* is diverse, it apparently should continue to be placed in Gynotrocheae, along with *Gynotroches* and *Pallacalyx*.

The four mangrove genera—*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*—share the following synapomorphies: endothelium not formed, outer integument vascularized, endosperm overflowing, viviparous seedlings, testa not differentiated histologically, and tegmen lacking. Thus, the

mangrove genera undoubtedly form a coherent group, Rhizophoreae. Wood anatomy (van Vliet, 1976), leaf architecture (Keating & Randriana-solo, this volume), leaf anatomy (particularly stomatal type; Baas, pers. comm.), and consistent distinct chromosome number ( $2n = 36$ ; Yoshioka et al., 1984) also support the coherence of Rhizophoreae. The cladistic analysis indicates that Rhizophoreae have direct relationships with Gynotrocheae (not including *Crossostylis*), rather than with Macarisieae.

On the basis of our cladistic analysis, we suggest the following revised classification:

Family Rhizophoraceae (not including Anisophylleaceae)

Tribe Macarisieae

Subtribe Cassipourinae

*Blepharistemma*

*Cassipourea*

*Comiphyton*

Subtribe Macarisinae

*Anopyxis*

*Macarisia*

*Sterigmapetalum*

Tribe Crossostylideae

*Crossostylis*

Tribe Gynotrocheae

Subtribe Carallinae

*Carallia*

Subtribe Gynotrochinae

*Gynotroches*

*Pellacalyx*

Tribe Rhizophoreae

*Bruguiera*

*Ceriops*

*Kandelia*

*Rhizophora*

#### LITERATURE CITED

- ADATIA, R. D. & S. G. GAVDE. 1962. Embryology of the Celastraceae. In: Plant Embryology—A Symposium 1–11. Nov. 11–14, 1960. CSIR, New Dehli.
- AIRY SHAW, H. K. 1973. J. C. Willis' a Dictionary of the Flowering Plants and Ferns, 8th edition. Cambridge Univ. Press, Cambridge.
- ALSTON, A. H. G. 1925. Revision of the genus *Cassipourea*. Bull. Misc. Inform. (Kew Bull.) 1925: 241–276.
- ARÈNES, J. 1954. Fam. 150. Rhizophoracées. In: H. Humbert (editor), Flore de Madagascar et des Comores. Typog. Firmin-Didot, Paris.
- BERKELEY, E. 1953. Morphological studies in the Celastraceae. J. Elisha Mitchell Sci. Soc. 69: 185–206.
- CAREY, G. 1934. Further investigations on the embryology of viviparous seeds. Proc. Linn. Soc. New South Wales 59: 392–410.
- COOK, M. T. 1907. The embryology of *Rhizophora mangle*. Bull. Torrey Bot. Club 34: 271–277.



- COPELAND, H. F. 1966. Morphology and embryology of *Euonymus japonica*. *Phytomorphology* 16: 326-334.
- CORNER, E. J. H. 1976. The Seeds of Dicotyledons. 2 volumes. Cambridge Univ. Press, Cambridge.
- CRONQUIST, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- . 1983. Some realignments in the dicotyledons. *Nordic J. Bot.* 3: 75-83.
- DAHLGREN, R. 1983. General aspects of angiosperm evolution and macrosystematics. *Nordic J. Bot.* 3: 119-149.
- . Rhizophoraceae and Anisophylleaceae: summary statement, relationships. *Ann. Missouri Bot. Gard.* (this volume).
- & R. F. THORNE. 1984. The order Myrtales: circumscription, variation, and relationships. *Ann. Missouri Bot. Gard.* 71: 633-699.
- ENDLICHER, S. 1840. *Genera Plantarum*. Vindobonae.
- FLORET, J. J. 1974. *Comiphyton*, genre nouveau Gabonais. *Adansonia* 14: 499-506.
- . 1976. A propos de *Comiphyton gabonense* (Rhizophoraceae—Macarisieae). *Adansonia* 16: 39-49.
- GEH, S. Y. & H. KENG. 1974. Morphological studies on some inland Rhizophoraceae. *Gard. Bull. Straits Settle.* 28: 183-220.
- GILL, A. M. & P. B. TOMLINSON. 1969. Studies on the growth of red mangrove (*Rhizophora mangle* L.) I. Habit and general morphology. *Biotropica* 1: 1-9.
- GRAHAM, S. A. 1964. The genera of Rhizophoraceae and Combretaceae in the Southeastern United States. *J. Arnold Arbor.* 45: 285-301.
- HABERLANDT, G. 1895. Über die Ernagrung der Keimlinge und die Bedeutung des Endospermes bei viviparen Mangrovepflanzen. *Ann. Jard. Bot. Buitenzorg* 12: 102-105.
- HOU, D. 1958. Rhizophoraceae. *In*: C. G. G. J. van Steenis (editor), *Flora Malesiana* 5: 429-493.
- . 1968. *Crossostylis* in the Solomon Islands and the New Hebrides (Rhizophoraceae). *Blumea* 16: 129-132.
- HYLAND, B. P. M. & M. J. E. COODE. 1982. A second species for Australian genus *Peripentadenia* (Elaeocarpaceae). *Kew Bull.* 3: 741-745.
- JUNCOSA, A. M. 1982. Developmental morphology of the embryo and seedling of *Rhizophora mangle* L. (Rhizophoraceae). *Amer. J. Bot.* 69: 1599-1611.
- . 1984a. Embryogenesis and seedling development in *Cassipourea elliptica* (Sw.) Poir. (Rhizophoraceae). *Amer. J. Bot.* 71: 170-179.
- . 1984b. Embryogenesis and developmental morphology of the seedling in *Bruguiera exaristata* Ding Hou (Rhizophoraceae). *Amer. J. Bot.* 71: 180-191.
- & P. B. TOMLINSON. 1987. Floral development in mangrove Rhizophoraceae. *Amer. J. Bot.* 74: 1263-1279.
- & ———. A historical and taxonomic synopsis of Rhizophoraceae and Anisophylleaceae. *Ann. Missouri Bot. Gard.* (this volume a).
- & ———. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophylleaceae. *Ann. Missouri Bot. Gard.* (this volume b).
- KARSTEN, G. 1891. Über die Mangrove-Vegetation im malayische Archipel. Eine morphologische-biologische Studie. *Biblioth. Bot. (Stuttgart)* 22: 11-18, 31-41.
- KEATING, R. C. & V. RANDRIANASOLO. Leaf architecture and relationships in the Rhizophoraceae and Anisophylleaceae. *Ann. Missouri Bot. Gard.* (this volume).
- LERSTEN, N. R. & J. D. CURTIS. 1974. Colleter anatomy in red mangrove, *Rhizophora mangle* (Rhizophoraceae). *Canad. J. Bot.* 52: 2277-2278.
- MAURITZON, J. 1934. Zur Embryologie der Elaeocarpaceae. *Arkiv Bot.* 26: 1-8.
- . 1936. Zur Embryologie und systematischen Abgrenzung der Reihen Terebinthales und Celastrales. *Bot. Not.* 1936: 161-212.
- . 1939. Contributions to the embryology of the orders Rosales and Myrtales. *Acta Univ. Lund.* 35: 1-121.
- MELCHIOR, H. 1964. Rhizophoraceae. *In*: H. Melchior (editor), *A. Engler's Syllabus der Pflanzenfamilien*. II. 2: 357-359.
- METCALFE, C. R. & L. CHALK. 1950. *Systematic Anatomy of the Dicotyledons*. 2 volumes. Clarendon Press, Oxford.
- RIDLEY, H. N. 1922. *The Flora of Malay Peninsula*. 1. L. Leeve & Co., London.
- . 1930. *The Dispersal of Plants Throughout the World*. L. Leeve & Co., London.
- SCHIMPER, A. F. W. 1893. Rhizophoraceae. *In*: A. Engler & K. Prantl, *Die Natürlichen Pflanzenfamilien*. 3: 42-56.
- SCHMID, R. 1986. On Cornerian and other terminology of angiospermous and gymnospermous seed coats: historical perspective and terminological recommendations. *Taxon* 35: 476-491.
- SPRAGUE, T. A. & L. A. BOODLE. 1909. Kokoti (*Anopyxis ealaensis* Sprague). *Bull. Misc. Inform. (Kew Bull.)* 1909: 309-312.
- STEYERMARK, J. A. & R. LIESNER. 1983 [1984]. Revision of the genus *Sterigmapetalum* (Rhizophoraceae). *Ann. Missouri Bot. Gard.* 70: 179-193.
- TOBE, H. & P. H. RAVEN. 1983. An embryological analysis of the Myrtales: its definition and characteristics. *Ann. Missouri Bot. Gard.* 70: 71-94.
- & ———. 1987a. The embryology and relationships of *Cassipourea* and *Sterigmapetalum* (Rhizophoraceae—Macarisieae). *Opera Bot.* 92: 253-264.
- & ———. 1987b. Systematic embryology of the Anisophylleaceae. *Ann. Missouri Bot. Gard.* 74: 1-26.
- & ———. Floral morphology and evolution in Anisophylleaceae. *Bot. J. Linn. Soc.* 97 (in press).
- TOMLINSON, P. B., R. B. PRIMACK & J. S. BUNT. 1979. Preliminary observations on floral biology in mangrove Rhizophoraceae. *Biotropica* 11: 256-277.
- VAN DER PIJL, L. 1969. *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin.
- VAUGHAN, J. G. 1970. *The Structure and Utilization of Oil Seeds*. Chapman & Hall Ltd., London.
- , & J. M. WHITEHOUSE. 1971. Seed structure and the taxonomy of the Cruciferae. *Bot. J. Linn. Soc.* 64: 383-409.
- VENKATA RAO, C. 1953. Floral anatomy and embryology of two species of *Elaeocarpus*. *J. Indian Bot. Soc.* 32: 21-33.
- VERKERKE, W. 1985. Ovules and seeds of the Polygalaceae. *J. Arnold Arbor.* 66: 353-394.



VLIET, G. J. C. M. VAN. 1976. Wood anatomy of the Rhizophoraceae. Leiden Bot. Ser. 3: 20-75.

WEIBEL, R. 1968. Morphologie de l'embryon et de la graine des *Elaeocarpus*. Candollea 23: 101-108.

YOSHIOKA, H., K. KONDO, M. SEGAWA, K. NEHIRA & S. MAEDA. 1984. Karyomorphological studies in five species of mangrove genera in the Rhizophoraceae. La Kromosomo II-35-36: 1111-1116.